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That "darned *Dorsiceratus* case" (Copepoda, Harpacticoida, Cletodidae T. Scott)—an attempt of a systematic approach, including the description of three new species

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Abstract

Despite the generally recognised importance of Copepoda Harpacticoida in aquatic ecosystems, our knowledge of that taxon is still very patchy and even marginal with regard to deep-sea representatives. Nonetheless, studies over the past decades have shown that deep-sea Harpacticoida present an almost overwhelming diversity of species. In order to obtain a most realistic assessment of this, taxonomic studies are essential in addition to faunistic ones. They reveal that particularly rare deep-sea groups can be characterised by a large number of different species even from the same location. One such rare group is the taxon *Dorsiceratus* Drzycimski, a representative of the so-called *Ceratonotus* group (Cletodidae T. Scott). The five species known to date, namely *Dorsiceratus dinah* George & Plum, *Do. octocornis* Drzycimski, *Do. triarticulatus* Coull, *Do. ursulae* George, and *Do. wilhelminae* George & Plum, indicate a worldwide distribution of *Dorsiceratus*. On the one hand, they are characterised by very similar morphological features. Simultaneously, however, derived characters occur very scattered, making a clear characterisation of both the species and a monophylum *Dorsiceratus* difficult. The aim of the present morphological comparison is to substantiate a monophylum *Dorsiceratus* and also to characterise the species known to date. For this purpose, we studied *Dorsiceratus* specimens collected from various marine areas over the past 26 years. The monophyly of *Dorsiceratus* can be justified by the following autapomorphies: (1) mandibular palpus without basal seta 1, (2) P2 enp2 with 1 apical seta, (3) P2 exp3 with tube pore, (4) P4 endopod sexually dimorphic. The species can also be characterised by at least one autapomorphy each. Among a total of 57 individuals we studied, we assigned 12 to three new species: *Do. andeep* **sp. nov.**, *Do. denizae* **sp. nov.**, and *Do. karinae* **sp. nov.**, and one male specimen appears to resemble *Do. ursulae*. However, the remaining 44 individuals could not be morphologically assigned to any of the known or new species. They were provisionally assigned to eight different morphotypes and a heterogeneous morpho-group, which, however, cannot be justified phylogenetically. According to our results, morphological comparison alone is not sufficient for an unambiguous assignment of future findings to *Dorsiceratus*. It needs to be supplemented by molecular analyses. A diagnostic key to species is provided.

Key Words

Cletodinae, deep sea, meiofauna, morphology, seamounts, systematics, taxonomy

Introduction

Copepoda Harpacticoida (Crustacea) are among the most important representatives of marine meiofauna alongside the Nematoda (George et al. 2020). Their species diversity, their numbers, and their ecological importance have even led to them being referred to not as "insects of the sea" (like e.g., Huys and Boxshall

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1991) but, conversely, insects as "terrestrial copepods" (Schminke 2007).

In the deep sea, the largest contiguous habitat on earth, an enormous diversity of Harpacticoida species has been identified to date (George 1999, 2005; Rose et al. 2005; George et al. 2014, 2018). Nevertheless, our knowledge of the deep-sea meiofauna in general and the deep-sea Harpacticoida in particular is still very incomplete. And especially for rare taxa such as the representatives of the *Ceratonotus* group (Cletodidae T. Scott, 1905), our knowledge is marginal at best; sampling from the depths of the oceans yields a proportion of > 80% to 99% of previously unknown harpacticoid species (e.g., George and Schminke 2002, George 2005, George et al. 2014, 2018)! This shows the great importance of the taxonomic recording of (deep-sea) harpacticoids, because only this provides the prerequisites for an exhaustive inventorying as a basis for chorological, phylogenetic, and biogeographical studies, which in turn promote our understanding of the interrelationships of life in the deep sea.

The genus *Dorsiceratus* Drzycimski, 1967 (Copepoda, Harpacticoida, Cletodidae T. Scott, 1904) was established by Drzycimski (1967) in the context of the description of a species found in the Korsfjord (Norway), *Do. octocornis* Drzycimski, 1967. That author assigned *Do. octocornis* to the Ancorabolidae Sars, 1909, and within this family to the Ancorabolinae Lang, 1948, because *Do. octocornis*, like the other taxa known at the time (*Ancorabolus* Norman, 1903, *Arthropsyllus* Sars, 1909, *Ceratonotus* Sars, 1909, *Echinocletodes* Lang, 1936, and *Echinopsyllus* Sars, 1909), was characterised by the transversely strongly extended basis of the first swimming leg. Since then, the systematics of the Ancorabolidae have undergone a series of studies (see detailed literature lists in George 2020, 2021), which recently led to the transfer of some of their representatives, summarised as the *Ceratonotus* group (cf. Conroy-Dalton 2001), from the Ancorabolidae to the Cletodidae (George 2020).

Dorsiceratus currently comprises five described species. Like most deep-sea Harpacticoida, representatives of this genus are rarely encountered. Drzycimski (1967) had only two females and one male for his species description. The type material of the second described species, *Do. triarticulatus* Coull, 1973, also consists of only two females and one male (Coull 1973). The third species, *Do. ursulae* George, 2006, was described 33 years later; here the type material comprised just two females and two copepodids (CII, CIV) (George 2006a). The two most recently described species, *Do. dinah* George & Plum, 2009, and *Do. wilhelminae* George & Plum, 2009, are each based on only one female (George and Plum 2009). These two circumstances—the rare findings of *Dorsiceratus* and the small number of individuals available for the description of these species—are essential barriers for the study on the systematics of this taxon. As already mentioned on various occasions (e.g., George 1998a, b, 2006a; Conroy-Dalton 2001), such a low yield of individuals means that intraspecific variability cannot be detected. The present "darned *Dorsiceratus* case" provides a clear example of this, especially when the circumstances mentioned are exacerbated on the one hand by a generally conservative expression of characters and on the other hand by a heterogeneous occurrence of modified characters. This is the moment when morphological studies may have actually reached their limits and must necessarily be supplemented by molecular methods in order to create clarity.

However, it was not possible to use molecular methods in this study, as the available *Dorsiceratus* material mostly comes from expeditions that took place up to 26 years ago and in which formalin was always used for sample fixation. Only one specimen found on the IceDIVA cruise (2021) could be used to obtain DNA data (Frederic Bonk, pers. comm.). To our knowledge, this is the first individual of the genus worldwide for which genetic information would become available.

Despite the above-mentioned adversities, we have attempted to contribute to the clarification of the systematic characterisation of *Dorsiceratus* and to determine species by means of the classical morphological approach. In addition to the available species (re-) descriptions (Drzycimski 1967; Coull 1973; George 2006a; George and Plum 2009) and the accessible type material, 57 adult individuals were used, all of which could be unequivocally assigned to the taxon *Dorsiceratus*. They originate from samples collected on various research cruises in the Atlantic, Pacific, and Southern Oceans and eastern Mediterranean in the years 1998–2021 (Fig. 1, Table 1). All specimens were found in the deep sea (from 675 down to 5,495 m depth), some of them on Atlantic and Mediterranean seamounts. The morphological comparison of the animals made it possible to describe three further species—an updated key to the species is provided—and also to identify eight further different morphotypes and one "morpho-group" (Table 2). Due to their low occurrence, combined with their (partly) poor condition, the morphotypes could be defined but not described.

Nonetheless, in addition to the three species descriptions, an attempt is made to substantiate the characterisation of all known species and the different morphotypes and to evaluate characters with regard to their possibly intraspecific variable occurrence. However, due to the available characters and their states, it is not possible to consider exclusively phylogenetic criteria. In particular, the grouping of individuals into different morphotypes could only be carried out typologically. In that context, the morpho-group is formed by a rather heterogeneous grouping of individuals that resemble each other but are not characterised by clear (derived) characteristic similarities.

The hypotheses and conclusions presented here may nevertheless serve as a basis for future studies on *Dorsiceratus* that should urgently incorporate molecular methods.

Table 1. List of the species/specimens that were compared in the present study. The list is presented chronologically according to the expeditions carried out, and the individuals are assigned to their respective finding places (locality, station, geographical position, depth, date, sampling gear). In the last column, the corresponding literature reference is given.

Studied specimens	F	M	Locality	Station	Geographical position	Depth (m)	Date	Gear	Reference
M42/3 (1998): Northeastern Atlantic									
Do. 57: "*D. ursulae*" (PT) (George 2006)	1		Great Meteor Seamount GMS	#548	29°52.8'N, 28°14.2'W	2320	9/16/1998	MUC	George (2006)
DIVA 1 (2000): Southeastern Atlantic									
Do. 1	1		Central Angola Basin AB_C	#325/5-12	19°58.2'S, 02°59.6'E	5495	7/14/2000	MUC	Present study
Do. 2	1		Central Angola Basin AB_C	#325/7-3	19°58.2'S, 02°59.8'E	5494	7/14/2000	MUC	Present study
Do. 3: *D. denizae* sp. nov. (PT2)	1		Central Angola Basin AB_C	#325/7-4	19°58.2'S, 02°59.8'E	5494	7/14/2000	MUC	Present study
Do. 4		1	Central Angola Basin AB_C	#331/1-10	19°07.0'S, 03°52.0'E	5470	7/18/2000	MUC	Present study
Do. 5	1		Central Angola Basin AB_C	#340	18°17.3'S, 04°41.2E–18°19.3'S, 04°41.8'E	5419–5443	7/23/2000	EBS	Present study
Do. 6	1		Central Angola Basin AB_C	#341/1	17°08.0'S, 04°42.0'E	5466	7/23/2000	BC	Present study
Do. 7	1		Central Angola Basin AB_C	#346/1-1	16°17.0'S, 05°27.0'E	5432	7/27/2000	MUC	Present study
Do. 8	1		Central Angola Basin AB_C	#346/1-4	16°17.0'S, 05°27.0'E	5432	7/27/2000	MUC	Present study
Do. 9	1		Central Angola Basin AB_C	#346/2-9	16°17.0'S, 05°27.0'E	5389	7/27/2000	MUC	Present study
Do. 10	1		Central Angola Basin AB_C	#346/2-9	16°17.0'S, 05°27.0'E	5389	7/27/2000	MUC	Present study
Do. 11	1		Central Angola Basin AB_C	#346/2-11	16°17.0'S, 05°27.0'E	5389	7/27/2000	MUC	Present study
Do. 12		1	Central Angola Basin AB_C	#346/2-12	16°17.0'S, 05°27.0'E	5389	7/27/2000	MUC	Present study
Do. 13		1	Central Angola Basin AB_C	#346/3-3	16°17.0'S, 05°27.0'E	5389	7/27/2000	MUC	Present study
Do. 14	1		Central Angola Basin AB_C	#346/4-2	16°16.9'S, 05°27.0'E	5389	7/27/2000	MUC	Present study
Do. 15	1		Central Angola Basin AB_C	#346/4-11	16°16.9'S, 05°27.0'E	5389	7/27/2000	MUC	Present study
Do. 16	1		Central Angola Basin AB_C	#346/5-4	16°16.9'S, 05°27.0'E	5389	7/27/2000	MUC	Present study
Do. 17: *D. denizae* sp. nov. (HT)	1		Central Angola Basin AB_C	#346/5-9	16°16.9'S, 05°27.0'E	5389	7/27/2000	MUC	Present study
Do. 18	1		Central Angola Basin AB_C	#346/6-10	16°17.0'S, 05°27.0'E	5389	7/27/2000	MUC	Present study
Do. 19	1		Central Angola Basin AB_C	#346/6-11	16°17.0'S, 05°27.0'E	5389	7/27/2000	MUC	Present study
Do. 20: *D. denizae* sp. nov. (PT1)	1		Central Angola Basin AB_C	#346/8-1	16°17.0'S, 05°27.0'E	5390	7/27/2000	MUC	Present study
Do. 21		1	Central Angola Basin AB_C	#346/8-4	16°17.0'S, 05°27.0'E	5390	7/27/2000	MUC	Present study
Do. 22	1		Central Angola Basin AB_C	#346/8-6	16°17.0'S, 05°27.0'E	5390	7/27/2000	MUC	Present study
Do. 23	1		Central Angola Basin AB_C	#346/8-6	16°17.0'S, 05°27.0'E	5390	7/27/2000	MUC	Present study
Do. 24		1	Central Angola Basin AB_C	#346/8-8	16°17.0'S, 05°27.0'E	5390	7/27/2000	MUC	Present study
Do. 25		1	Central Angola Basin AB_C	#346/8-9	16°17.0'S, 05°27.0'E	5390	7/27/2000	MUC	Present study
ANDEEP II (2002): Northwestern Weddell Sea									
Do. 37		1	East of Antarctic Peninsula	#133/8-A	65°20.09'S, 54°14.72'W	1108	3/7/2002	MUC	Present study
Do. 38: *D. andeep* sp. nov. (HT)	1		East of Antarctic Peninsula	#133/8-C	65°20.09'S, 54°14.72'W	1108	3/7/2002	MUC	Present study
Do. 39		1	East of Antarctic Peninsula	#133/10-A	65°20.30'S, 54°14.67'W	1110	3/7/2002	MUC	Present study
Do. 40		1	East of Antarctic Peninsula	#133/10-A	65°20.30'S, 54°14.67'W	1110	3/7/2002	MUC	Present study
NODINAUT (2004): Northeastern Pacific									
Do. 41	1		Clarion Clipperton Zone CCZ	#11/8	14°2.94'N, 130°4.73'W	5035	6/1/2004	MUC	Mahatma (2009)
DIVA 2 (2005): Southeastern Atlantic									
Do. 26	1		Northern Angola Basin AB_N	#46/10	9°55.9'S, 0°53.8'E	5651	3/11/2005	MUC	Present study
Do. 27	1		Eastern Guinea Basin GB_E	#56/1	0°0.0'S, 2°25.0'W	5064	3/14/2005	MUC	Present study
Do. 28	1		Eastern Guinea Basin GB_E	#57/4	0°0.1'S, 2°25.0'W	5063	3/14/2005	MUC	Present study
Do. 29		1	Eastern Guinea Basin GB_E	#57/9	0°0.1'S, 2°25.0'W	5063	3/14/2005	MUC	Present study
Do. 30	1		Eastern Guinea Basin GB_E	#58/10	0°0.0'S, 2°25.0'W	5060	3/14/2005	MUC	Present study

Studied specimens	F	M	Locality	Station	Geographical position	Depth (m)	Date	Gear	Reference
Do. 31	1		Eastern Guinea Basin GB_E	#60/5	0°0.0'S, 2°25.1'W	5063	3/15/2005	MUC	Present study
Do. 32	1		Eastern Guinea Basin GB_E	#62/10	0°0.0'S, 2°25.0'W	5062	3/15/2005	MUC	Present study
Do. 33		1	Eastern Guinea Basin GB_E	#62/10	0°0.0'S, 2°25.0'W	5062	3/15/2005	MUC	Present study
Do. 34: aff. *D. ursulae* George, 2006		1	Western Guinea Basin GB_{W1}	#76/10	0°50.0'N, 5°35.0'W	5142	3/19/2005	MUC	Present study
Do. 35		1	Western Guinea Basin GB_{W1}	#78/6	0°50.1'N, 5°35.1'W	5136	3/19/2005	MUC	Present study
Do. 36		1	Western Guinea Basin GB_{W1}	#80/5	0°50.0'N, 5°35.0'W	5138	3/19/2005	MUC	Present study
Do. 48		1	Western Guinea Basin GB_{W2}	#100/6	0°37.2'N, 6°28.1'W	5167	3/23/2005	MUC	Present study
M71/1 (2006): Eastern Mediterranean Sea									
Do. 42		1	Anaximenes Seamount	#930-2	35°26.06'N, 30°09.88'E	675	12/19/2006	MUC	George et al. (2018)
Do. 43	1		Anaximenes Seamount	#930-3	35°26.06'N, 30°09.88'E	675	12/19/2006	MUC	George et al. (2018)
Do. 44		1	Anaximenes Seamount	#930-5	35°26.06'N, 30°09.88'E	675	12/19/2006	MUC	George et al. (2018)
Do. 45		1	Anaximenes Seamount	#930-11	35°26.06'N, 30°09.88'E	675	12/19/2006	MUC	George et al. (2018)
DIVA 3 (2009): Southwestern Atlantic									
Do. 46		1	Brazil Basin	#558	26°33.95'S, 035°13.33'W – 26°33.79'S, 035°13.32'W	4481–4479	7/23/2009	EBS	Present study
MSM14/1 (2009/2010): Eastern Mediterranean Sea									
Do. 49: *D. karinae* sp. nov., PT4	1		Eratosthenes Seamount EratoS	#1095/6-10	33°38.11'N, 32°32.62'E	943	12/26/2009	MUC	Present study
Do. 50: *D. karinae* sp. nov., PT7	1		Eratosthenes Seamount EratoS	#1095/6-12	33°38.11'N, 32°32.62'E	943	12/26/2009	MUC	Present study
Do. 51: *D. karinae* sp. nov., PT3		1	Eratosthenes Seamount EratoS	#1095/7-1	33°38.11'N, 32°32.62'E	943	12/26/2009	MUC	Present study
Do. 52: *D. karinae* sp. nov., PT6		1	Eratosthenes Seamount EratoS	#1095/7-2	33°38.11'N, 32°32.62'E	943	12/26/2009	MUC	Present study
Do. 53: *D. karinae* sp. nov., HT	1		Eratosthenes Seamount EratoS	#1100/1-4	33°47.13'N, 32°46.11'E	906	12/27/2009	MUC	Present study
Do. 54: *D. karinae* sp. nov., PT5	1		Eratosthenes Seamount EratoS	#1112/7-1	33°37.48'N, 32°46.53'E	875	12/29/2009	MUC	Present study
Do. 55: *D. karinae* sp. nov., PT1 (AT)		1	Eratosthenes Seamount EratoS	#1112/8-3	33°37.47'N, 32°46.53'E	874	12/29/2009	MUC	Present study
Do. 56: *D. karinae* sp. nov., PT2		1	Eratosthenes Seamount EratoS	#1112/8-3	33°37.47'N, 32°46.53'E	874	12/29/2009	MUC	Present study
IceDIVA (2021): Northeastern Atlantic									
Do. 47	1		West of Madeira	#39-1	36°02.367'N, 18°59.499'W – 36°02.136'N, 19°00.736'W	5488–5487	1/20/2021	EBS	Present study

Table 2. List of the compared individuals and their assignment to the corresponding species, morphotypes, or morpho-group according to the most obvious morphological characters. **Sex** = F: female, M: male; **BL (µm)** = body length; **FR l/w** = furcal rami length/width ratio; **P1 exp right/left segs.** = no. of segments on the right/left exopod, (s) = suture discernible; **P1 Exp** = setae/spines on exopodal segments; **P2, P3, P4 Exp-3** = no. of setae/spines on third exopodal segment of P2, P3, and P4, TP = tube pore; **P5 benp/exp** = P5 basoendopod and exopod distinct (d) or fused (f); **P5 benp setae/TPs** = no. of setae/tube pores on P5 basoendopod.

No.	No. species /morphotypes	Species/specimen	Sex	BL (µm)	FR l/w	P1 exp right/left segs.	P1 Exp	P2 Exp-3	P3 Exp-3	P4 Exp-3	P5 benp/exp	P5 benp setae/TPs
	1	*Do. ursulae*	F	360	6/1	**2(s):2(s)**	0-1; 0-2-III	1-2-II+TP	2-2-II**+TP**	1-2-II**+TP**	d	2/2
1		*Do.* 34 *(Do.* aff. *ursulae)*	M	487	5/1	**2(s):2(s)**	0-1; 0-2-III	1-2-II+TP	2-2-II**+TP**	1-2-II**+TP**	d	2/2
	2	*Do. octocornis*	F	470	4/1	**2:2**	0-1; 0-2-III	1-2-II+TP	2-2-II**+TP**	1-2-II**+TP**	**f**	**1**/2
			M	?	4/1	**2:2**	0-1; 0-2-III	1-2-II+TP	2-2-II**+TP**	1-2-II**+TP**	d	**1**/2
	3	*Do. wilhelminae*	F	395	4/1	**2:2**	0-1; 0-2-III**+TP**	1-2-II+TP	2-2-II**+TP?**	1-2-II**+TP**	d	2/2
	4	*Do. dinah*	F	380	4/1	**2:2**	0-1; 0-2-III**+TP**	1-2-II+TP	2-2-II**+TP**	1-2-II**+TP**	**f**	**1/1**
	5	*Do. triarticulatus*	F	670	7/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	**0/0**
			M	470	?	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II+**2TP**	1-2-II	d	2/2
2	***6 Do. karinae* sp. nov.**	*Do.* 53 (HT)	F	547	4/1	**2:2**	0-1; 0-2-III	1-2-II+TP	2-2-II**+TP**	1-2-II	d	2/**1**
3		*Do.* 55 (PT1/AT)	M	401	5/1	**2:2**	0-1; 0-2-III	1-2-II+TP	2-2-II**+TP?**	1-2-II	d	2/**1**
4		*Do.* 56 (PT2)	M	352	5/1	**2:2**	0-1; 0-2-III	1-2-II+TP	2-2-II**+TP?**	1-2-II	d	2/**1**
5		*Do.* 51 (PT3)	M	368	4/1	**2:2**	0-1; 0-2-III	1-2-II+TP	2-2-II**+TP**	1-2-II	d	2/**1**
6		*Do.* 49 (PT4)	F	482	4/1	**2:2**	0-1; 0-2-III	1-2-II+TP	2-2-II**+TP**	1-2-II	d	2/**1**
7		*Do.* 54 (PT5)	F	422	5/1	**2:2**	0-1; 0-2-III	1-2-II+TP	2-2-II**+TP**	1-2-II	d	2/**1**
8		*Do.* 52 (PT6)	M	376	5/1	**2:2**	0-1; 0-2-III	1-2-II+TP	2-2-II**+TP?**	1-2-II	d	2/**1**
9		*Do.* 50 (PT7)	F	454	5/1	**2:2**	0-1; 0-2-III	1-2-II+TP	2-2-II**+TP?**	1-2-II	d	2/**1**
10	***7 Do. denizae* sp. nov.**	*Do.* 17 (HT)	F	686	7/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	**1**/2
11		*Do.* 20 (PT1)	F	747	7/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II**+TP**	1-2-II	d	**1**/2
12		*Do.* 3 (PT2)	F	718	7/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	**1**/2
13	***8 Do. andeep* sp. nov.**	*Do.* 38 (HT)	F	799	**8/1**	3:3	0-1; 0-1;0-2-II	**0**-2-II+TP	**0**-2-II**+TP**	**0**-2-II	d	2/**0?**
14	**Morphotype 1**	*Do.* 43	F	457	3/1	**2:2**	0-1; 0-2-III	1-2-II+TP	2-2-II	1-2-II**+TP**	d	**1/1?**
15		*Do.* 42	M	362	4/1	**2:2**	0-1; 0-2-III	1-2-II**+TP?**	2-2-II	1-2-II	d	**?/?**
16		*Do.* 44	M	371	4/1	**2:2**	0-1; 0-2-III	1-2-II+TP	2-2-II	1-2-II	d	**1/1**
17		*Do.* 45	M	414	4/1	**2:2**	0-1; 0-2-III	1-2-II**+TP?**	2-2-II	1-2-II	d	**1/1?**
18	**Morphotype 2**	*Do.* 26	F	631	**8/1**	broken	broken	1-2-II+TP	2-2-II	1-2-II	d	**1/1**
19	**Morphotype 3**	*Do.* 41	F	698	**7/1**	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	**f**	2/**0**
20	**Morphotype 4**	*Do.* 15	F	590	6/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II**+TP**	1-2-II	d	2/2
21		*Do.* 11	F	596	5/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II**+TP**	broken	d	2/2
22	**Morphotype 5**	*Do.* 23	F	612	4/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/**1**
23		*Do.* 18	F	577	3/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/**1**
24	**Morphotype 6**	*Do.* 4	M	?	broken	3:3	0-1; 0-1;0-2-II	broken	2-2-II	broken	d	**1/1**
25		*Do.* 13	M	536	6/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	**1/1**
26		*Do.* 21	M	515	6/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	**1/1**
27		*Do.* 12	M	576	6/1	**3:2**	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	**1/1**
28		*Do.* 25	M	519	5/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	**1/1**
29		*Do.* 29	M	495	5/1	3:?	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	**1/1**
30		*Do.* 46	M	514	5/1	**3:2(s)**	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	**1/1**
31		*Do.* 33	M	541	4/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	**1/1**
32	**Morphotype 7**	*Do.* 28	F	595	4/1	**2(s):3**	0-1; 0-2-III**+TP**	1-2-II+TP	2-2-II	1-2-II	d	2/2
33	**Morphotype 8**	*Do.* 48	M	569	7/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II+**2TP**	1-2-II	d	**1/1**
34	**"Morpho-group" 9**	*Do.* 37	M	563	9/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d?	**?/?**
35		*Do.* 39	M	555	7/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	**1/1?**
36		*Do.* 40	M	575	7/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	**1/1?**
37		*Do.* 2	F	730	6/1	3:?	0-1; 0-1;0-2-II	broken	broken	broken	d	broken
38		*Do.* 10	F	868	6/1	**3:2**	0-1; 0-1;0-2-II	1-2-II+TP	?-?-?	broken	d	2/2
39		*Do.* 14	F	820	6/1	3:broken	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2
40		*Do.* 57 ("*D. ursulae*", paratype)	F	585	5/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2
41		*Do.* 36	M	547	5/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2?
42		*Do.* 27	F	715	5/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/?
43		*Do.* 9	F	669	5/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2
44		*Do.* 8	F	647	5/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2
45		*Do.* 1	F	635	5/1	3:3	0-1; 0-1;0-2-II	broken	broken	broken	d	2/2
46		*Do.* 19	F	610	5/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2
47		*Do.* 6	F	660	5/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	broken
48	**"Morpho-group" 9**	*Do.* 5	F	595	5/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	broken	broken	broken
49		*Do.* 22	F	563	5/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	broken
50		*Do.* 31	F	?	5/1	broken	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2
51		*Do.* 24	M	502	5/1	?:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2
52		*Do.* 7	F	603	4/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2
53		*Do.* 16	F	596	4/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2
54		*Do.* 30	F	618	4/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2
55		*Do.* 47	F	479	4/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2
56		*Do.* 32	F	971	4/1	broken:3	0-1; 0-1;0-2-II	broken	broken	broken	d	2/2
57		*Do.* 35	M	517	4/1	3:3	0-1; 0-1;0-2-II	1-2-II+TP	2-2-II	1-2-II	d	2/2

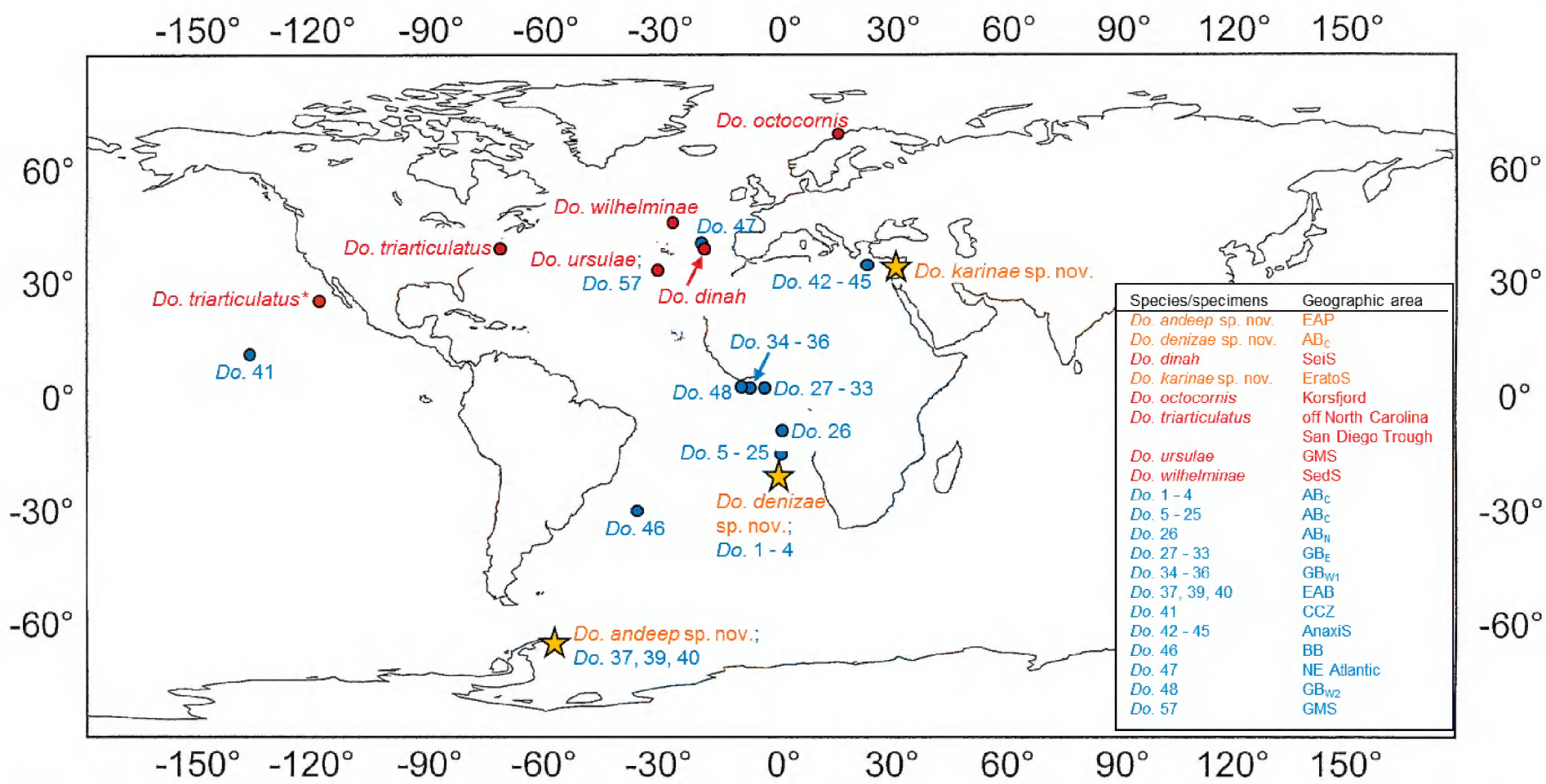

Figure 1. Map showing the geographical distribution of the so-far known *Dorsiceratus* species (red circles/names), the here described new species (yellow stars/names), and the further individuals studied in the present contribution (blue circles/numbers). The asterisk * in *Do. triarticulatus** refers to material reported by Thistle (1977, 1982) as "c.f. *Dorsiceratus*", subsequently identified as *Do. triarticulatus* by Conroy-Dalton (2001).

Materials and methods

Treatment of samples and material

Sampling was done at all cruises with a multiple corer (MUC), except for single stations, where specimens had been got as "bycatch" from the Brenke epibenthic sledge (EBS) (Brenke 2005) or the Boxcorer (BC) (cf. Table 1). The samples were fixed immediately on board in 4% buffered formalin. Due to the standard fixation of the material in formalin at that time, genetic studies could not be included in the here-presented systematic comparisons. Only the specimen collected on the IceDIVA cruise (2021) (Table 1: *Do.* #47) offers the possibility of molecular analysis, as it was preserved in ethanol.

Copepoda Harpacticoida were sorted and dissected under a Leica M 125 stereomicroscope; *Dorsiceratus* specimens were put on slides and embedded with glycerol for species determination. For that purpose, three different Leica microscopes were used: DMLS, DM 2500, and DMR, the latter two being compound microscopes equipped with differential interference contrast. Drawings were made with the use of a camera lucida on the Leica DMR and the Leica DM 2500. Creation of digital illustrations of the microscopic pencil drawings was made using ADOBE Illustrator CS6 and ADOBE Photoshop CC 2019.

Morphological comparison was based on the respective original species (re-)descriptions (Drzycimski 1967; Coull 1973; George 2006a; George and Plum 2009), on the examination of the type material of *Dorsiceratus andeep* sp. nov., *Do. denizae* sp. nov., *Do. dinah*, *Do. karinae* sp. nov., *Do. ursulae*, and *Do. wilhelminae*, as well as the 44 additional *Dorsiceratus* specimens on which this study is based.

As far as phylogenetic aspects could be considered, they strictly follow the concept of the consequent phylogenetics (Hennig 1982; Ax 1984, 1988, 1995; Sudhaus and Rehfeld 1992; Wägele 2001) as well as the principle of oligomerisation (cf. Huys and Boxshall 1991; Seifried 2003), which postulates that the reduction of segments/elements constitutes the relatively more derived state. General scientific terminology follows Lang (1948) with additional terms from Huys and Boxshall (1991). Phylogenetic terminology is used as defined by Hennig (1982) and Ax (1984). The terms "telson" and "furca" are adopted from Schminke (1976).

The type material of *Do. andeep* sp. nov., *Do. denizae* sp. nov., and *Do. karinae* sp. nov., as well as the additional *Dorsiceratus* material, is deposited at the Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt, Germany).

The English text was improved by using a free version of DeepL.

Abbreviations**: A1:** antennule; **A2:** antenna, **AB_C:** Central Angola Basin, **AB_N:** Northern Angola Basin, **ACST:** anterior cephalothoracic setular tufts, **aes:** aesthetasc, **AnaxiS:** Anaximenes Seamount, **AT:** allotype, **BB:** Brazil Basin, **BC:** box corer, **CCZ:** Clarion Clipperton Fracture Zone, **CLDP:** cephalothoracic laterodorsal processes, **CLVEa:** cephalothoracic anterior lateroventral extensions; **cphth:** cephalothorax, **DP1–DP3:** dorsal processes 1–3, ***Do.* 1–*Do.* 57:** *Dorsiceratus* individuals 1–57; **EAP:** Eastern Antarctic Peninsula, **EBS:** Brenke epibenthic sledge, **enp1–enp3:** endopodal segments 1–3, **EratoS:** Eratosthenes Seamount, **exp1–exp3:** exopodal segments 1–3,

FLH: frontolateral horns, **FR:** furcal ramus/rami, **GB_E:** Eastern Guinea Basin; **GB_{W1}, GB_{W2}:** Western Guinea Basin 1 and 2; **GDS:** genital double somite, **GMS:** Great Meteor Seamount, **HT:** holotype, **l/w ratio:** length-to-width ratio, **md:** mandible, **MUC:** multi corer, **mxl:** maxillula, **mx:** maxilla, **mxp:** maxilliped, **P1–P6:** swimming legs 1–6, **PT:** paratype, **SedS:** Sedlo Seamount, **SeiS:** Seine Seamount.

Analysed material of *Dorsiceratus*

Dorsiceratus karinae sp. nov.

The research cruise MSM-14/1 of RV MARIA S. MERIAN (December 17, 2009–January 14, 2010) to the Eratosthenes Seamount (eastern Mediterranean, south of Cyprus; Fig. 2A) (Christiansen et al. 2012) was used for analytical studies of the meiobenthic communities (Sevastou et al. 2012, 2013; George 2022), as well as to record and describe new meiobenthic species from this seamount (Yamasaki et al. 2018; George 2023). The harpacticoid material included 8 individuals (4 females, 4 males) of the genus *Dorsiceratus* (Table 1: *Do.* 49–*Do.* 56), found at three stations on the seamount (Fig. 2A). They obviously form a scientifically new species and are described in the following as *Dorsiceratus karinae* sp. nov. Besides the record of a few yet undescribed specimens from the Anaximenes Seamount by George et al. (2018) (as *Dorsiceratus* sp., cf. Table 1: *Do.* 42–*Do.* 45), the description of *Dorsiceratus karinae* sp. nov. proves to be the first documented representative of the genus for the Mediterranean Sea.

Dorsiceratus denizae sp. nov.

The two expeditions, M48/1 (DIVA 1; summer 2000) and M63/2 (DIVA 2; spring 2005), of RV METEOR had led to the Angola and Guinea deep-sea basins (Fig. 2B)

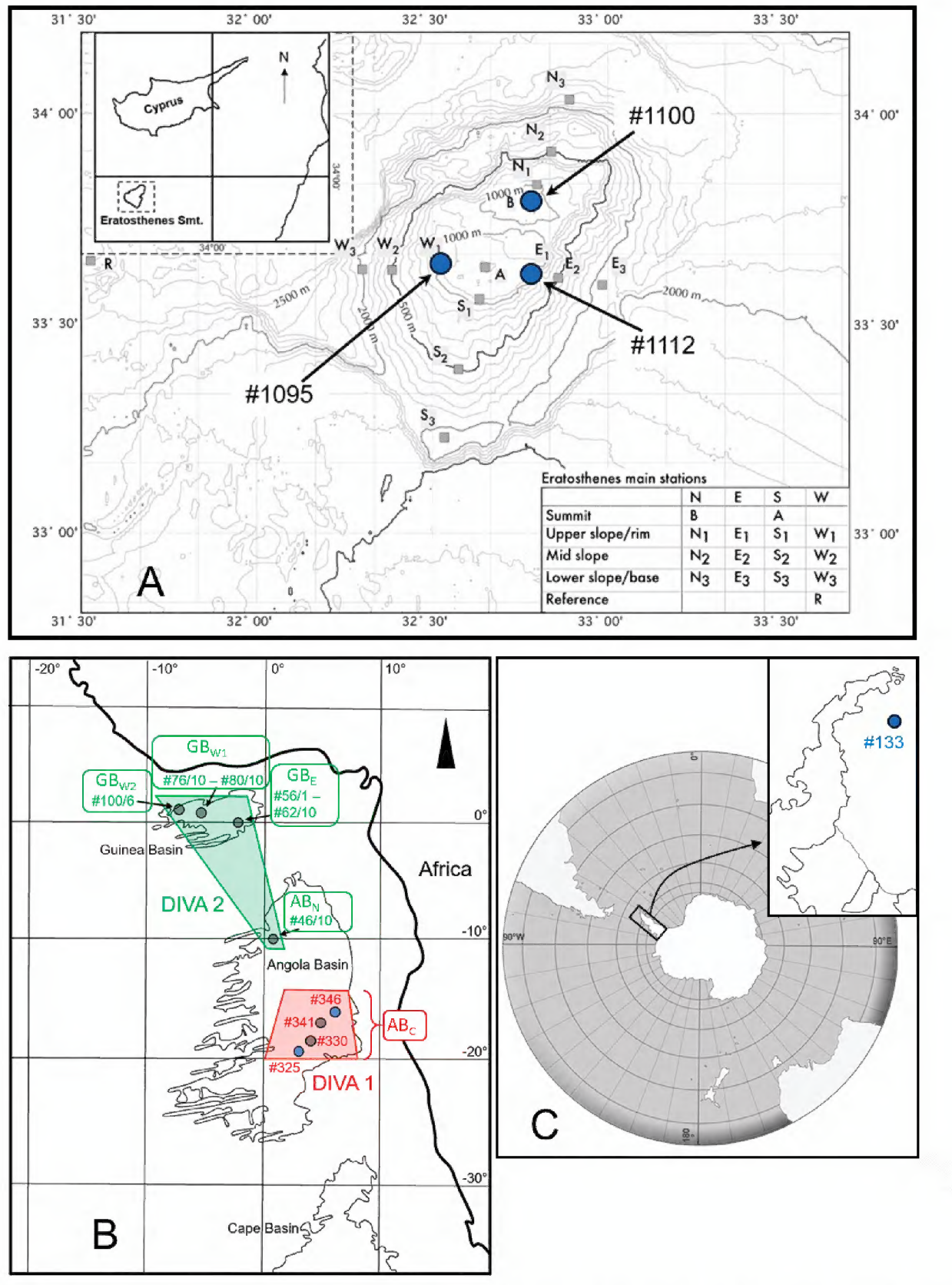

Figure 2. Maps showing the type locality of **A.** *Dorsiceratus karinae* sp. nov. (Eratosthenes Seamount, eastern Mediterranean Sea); **B.** *Do. denizae* sp. nov. (Central Angola Basin, southeastern Atlantic Ocean); **C.** *Do. andeep* sp. nov. (western Weddell Sea, Antarctica). Blue circles indicate the sampling stations of the corresponding species.

in the tropical southwest Atlantic (Martínez Arbizu and Schminke 2005; Balzer et al. 2006; Türkay and Pätzold 2009). The Angola Basin was sampled in the centre (AB_C) and north (AB_N), and the Guinea Basin in the east (GB_E) and at two sites in the west (GB_{W1}, GB_{W2}) (Fig. 2B).

Sampling of the meiofauna yielded a total of 26 *Dorsiceratus* specimens from the Angola Basin (DIVA 1: 19 females, 6 males; Table 1: *Do.* #1–*Do.* #25; DIVA 2: 1 female: *Do.* #26) and 11 specimens from the Guinea Basin (DIVA 2: 5 females, 6 males; Table 1: *Do.* 27–*Do.* 36 + *Do.* 48).

The description of *Do. denizae* sp. nov. is based on three specimens. The female holotype and two additional females (Table 1: *Do.* 3, *Do.* 17, *Do.* 20 = type material) were collected at the AB_C.

***Dorsiceratus andeep* sp. nov.**

As part of the ANDEEP I and II research projects (Brandt and Hilbig 2004), the western Weddell Sea (Fig. 2C) was sampled during the research cruise PS61 (ANTARKTIS-XIX/3–4) of RV POLARSTERN (Fütterer et al. 2003).

Of the Harpacticoida collected at station #133, east of the Antarctic Peninsula (EAB) (Fig. 2C), three males and one female could be unequivocally assigned to *Dorsiceratus* (Table 1: *Do.* 37–*Do.* 40).

The female (Table 1: *Do.* 38) differs from the males and the other individuals examined here in several respects to such an extent that it is described below as a new species.

Remaining *Dorsiceratus* material

In addition to the material from the above-listed tropical southeast Atlantic (37 individuals), the Eratosthenes Seamount (eight specimens), and the Antarctic Weddell Sea (four specimens), the following *Dorsiceratus* material (eight specimens) was used for the present study:

- Eastern Pacific, Clarion-Clipperton Fracture Zone (CCZ) (RV L'ATALANTE cruise NODINAUT, 2004; Mahatma 2009): 1 male (Table 1, Fig. 1: *Do.* 41);
- Eastern Mediterranean, Anaximenes Seamount (AnaxiS) (RV METEOR cruise M71/1, 2006; Christiansen et al. 2015): 1 female, 3 males (Table 1, Fig. 1: *Do.* 42–*Do.* 45);
- Tropical southwest-Atlantic, Brazil Basin (BB) (RV METEOR cruise M79/1, DIVA 3, 2009; Martínez Arbizu et al. 2015): 1 female (Table 1, Fig. 1: *Do.* 46);
- Subtropical northeast Atlantic, west of Madeira (RV SONNE cruise SO280, IceDIVA, 2021; Brix and Taylor 2021): 1 female (Table 1, Fig. 1: *Do.* 47).
- A re-examination of the type material of *Do. ursulae* revealed that the assigned female paratype (coll. no. UNIOL-2001.015/1; George 2006a) from the Great Meteor Seamount (GMS) does not belong to that species. It was therefore included in the present analysis (Table 1, Fig. 1: *Do.* 57).

Results

Taxonomy

Phylum: Arthropoda von Siebold, 1848
Subphylum: Crustacea Brünnich, 1772
Superclass: Multicrustacea Regier et al., 2010
Subclass: Copepoda Milne-Edwards, 1840
Order: Harpacticoida Sars, 1903
Family: Cletodidae T. Scott, 1905
Subfamily: Cletodinae George, 2021

Genus: *Dorsiceratus* Drzycimski, 1967

Type species. *Dorsiceratus octocornis* Drzycimski, 1967.

Additional species. *Do. andeep* sp. nov., *Do. denizae* sp. nov., *Do. dinah* George & Plum, 2009, *Do. karinae* sp. nov., *Do. triarticulatus* Coull, 1973, *Do. ursulae* George, 2006, *Do. wilhelminae* George & Plum, 2009.

Generic diagnosis (emended from George and Plum 2009): Cletodidae T. Scott, 1905; Cletodinae T. Scott, 1905; *Ceratonotus* group *sensu* Conroy-Dalton (2001). Body long, slender, ranging from 360 µm to 799 µm. Cphth frontally with strongly developed "peak", lacking pronounced frontolateral horns (FLH) but carrying anterior cephalothoracic setular tufts (ACST). Moreover, the lateral sides of the cphth are extended strongly in ventral direction (CLVEa). Rostrum constricted, fused to cphth, square or rectangular, sometimes more or less pronouncedly cleft at its tip, terminally with pair of sensilla and single tube pore (not documented for all species). Cphth and P2–P4-bearing thoracic somites dorsally with pair of spinulose cuticular processes at their distal margins, which bear single sensilla at their bases and tips (CLDP and DP1–DP3, respectively). Thoracic somites bearing P2–P5 with dorsal single tube pores, laterally with setular tufts (TST1–TST4). Genital double-somite present in female, dorsally with suture indicating former separation, anterior part (as well as P6-bering somite in male) dorsally with tube pore and with lateral setular tuft (GST). Abdominal part of GDS (likewise first abdominal male somite) and following abdominal somite also with lateral setular tufts (AST1, AST2). Last thoracic somite and abdominal somites dorsally without or with tube pores in differing numbers. Telson broader than long, trapezoidal in dorsal view. Anal operculum with row of spinules. FR of variable length, with 6–7 setae (I/II–VII), terminally with or without tube pore, furcal seta I minute or completely lost. Female A1 4-segmented, male A1 (5–?)6-segmented, haplo- or chirocer. A2 with allobasis bearing 2 abexopodal setae, exopod completely reduced. Md with variable gnathobase and 1-segmented palpus bearing 4–5 setae: 1 basal, 2–3 endopodal, and 1 exopodal seta. Mxl with coxa and basis distinct or fused. Mx with 2 endites, each with 2–3 setae, syncoxa and basis distinct or fused; endopod absorbed into basis, represented by 2 setae, or if distinct, then small and carrying 2 setae. Mxp prehensile, syncoxa

terminally with 1 seta, endopod produced into long claw accompanied by minute seta. Swimming legs 1–4 with transversely elongate bases and with exo- and endopod. P1 exopod 2–3-segmented; if 2-segmented, then exopodal outer spine of former exp2 arising at its original position or located subapically in terminal segment; thus, terminal segment with 4 or 5 (geniculate) setae. P1 endopod not prehensile, 2-segmented, enp2 terminally with 2 setae. P2–P4 with 3-segmented exopods and 2-segmented endopods, enp1 much shorter than enp2. P2 exp3 invariably with tube pore. Female endopodal segments P2–P4 with 1-2-2 apical setae, respectively. Male P2 endopod as in the female; P3 endopod 3-segmented, with outwardly curved apophysis on inner edge of enp2 and with 2 apical setae on enp3. Male P4 enp2 with 2 apical setae and 1 outer spine. P5 with basoendopod whose endopodal part is completely absorbed by the basis and represented by 0–2 setae that may be accompanied by 0–2 tube pores; outer basal seta arising from small setophore and accompanied by long tube pore; exopod distinct or fused to basoendopod, with 5 setae, 1 long tube pore may be present subterminally.

Dorsiceratus karinae sp. nov.

https://zoobank.org/7637BDC2-A981-45C3-A8C2-0DE04D643C8B

Figs 3–11

Locus typicus. northern plateau of the Eratosthenes Seamount, eastern Mediterranean Sea (33°47.13'N, 32°46.11'E, 906.0 m water depth), station #1100/1-4, where #1100 = station number, /1 = no. of MUC deployment (= replicate), -4 = no. of MUC-core.

Type material. • ***Holotype*:** female, collected on 27.12.2009 at type locality, put on one slide, collection number SMF-37284/1; • ***Paratype*** (PT) 1 (allotype): male, collected on 29.12.2009 at station #1112/8-3 (33°37.47'N, 32°46.53'E, 874.4 m water depth), put on one slide, collection number SMF-37285/1; • PT2: male, also collected at station #1112/8-3, put on one slide, collection number SMF-37286/1; • PT3: male, collected on 26.12.2009 at station #1095/7-1 (33°38.11'N, 32°32.62'E, 942.6 m water depth), put on one slide, collection number SMF-37287/1; • PT4: female, collected on 29.12.2009 at station #1095/6-10 (33°38.11'N, 32°32.62'E, 942.5 m water depth), put on one slide, collection number SMF-37288/1; • PT5: female, collected on 26.12.2009 at station #1112/7-1 (33°37.48'N, 32°46.53'E, 874.7 m water depth), put on one slide, collection number SMF-37289/1; • PT6: male, collected on 26.12.2009 at station #1095/7-2 (33°38.11'N, 32°32.62'E, 942.5 m water depth), put on one slide, collection number SMF-37290/1; • PT7: female, collected on 26.12.2009 at station #1095/6-12 (33°38.11'N, 32°32.62'E, 942.5 m water depth), distributed on three slides, collection number SMF-37291/1–3.

Etymology. the epitheton *karinae* is given in fond dedication to LT's mother, Mrs. Karin Tönjes (Apen, Germany). Gender: feminine.

Description of female. Habitus (Fig. 3A) slender and cylindrical, with inconspicuous boundary between pro- and urosome. Body length of holotype from rostral tip to end of FR 547 µm (mean 476 µm, range: 422–547 µm, n = 4), cphth and body somites dorsally with some sensilla and tube pores. Cphth and first three free thoracic somites dorsally with slender spinulose cuticular processes (CLDP, DT1–DT3) that bear a sensillum at their tips and are accompanied by another sensillum at their bases. Rostrum as in the male (Fig. 11A). Last thoracic and first abdominal somite fused into a GDS; former segmental demarcation still indicated by dorsal row of small spinules and pair of sensilla. Free thoracic body somites laterally with setular tufts, P6-bearing somite (= anterior half of GDS) additionally with tube pore. P2–P6-bearing somites dorsally also with 1 tube pore. First abdominal somite (= posterior half of GDS) and the following two abdominal somites dorsally with row of spinules at posterior margin; first and second abdominal somites additionally with pair of sensilla. Telson shorter than broad, slightly trapezoidal in shape from dorsal view. Anal operculum with some long spinules at its apical margin and basally flanked by a pair of sensilla.

FR (Fig. 3B) cylindrical and slender, about four times longer than broad, with 6 setae: seta I completely lost; seta II arising at outer margin halfway along the ramus; seta III broken in all eight specimens, but insertion clearly discernible, with a short tube pore next to it; seta IV minute, arising apically at the outer edge; seta V longest, located apically; seta VI as small as IV, positioned apically at inner edge of the ramus; seta VII arising dorsally at the end of the ramus.

A1 (Fig. 4A) 4-segmented, segments 1 and 3 of nearly the same length, second segment smaller, fourth segment about half the length of the third segment. First segment with row of long and flexible spinules at anterior margin and with 1 seta (broken in Fig. 4A) apically at anterior edge; second segment with 7 setae; third segment with 4 setae along anterior margin, at distal margin with 2 short setae and 1 aes that is accompanied by 1 long seta arising from acrothek; fourth segment with 11 setae, six of which biarticulated, and 2 setae accompanying an aes.

Setal formula: I–1; II–7; III–7 + aes; IV–11 + aes.

A2 (Fig. 4B, B*) with allobasis that carries 2 abexopodal setae but lacks an exopod; endopod with row of spinules proximally on the anterior and distally on the posterior margin; at its distal half it bears 4 long spinules and 3 setae, one of which bipinnate and the others bare. At its posterior edge, the endopod bears 2 cuticular frills (Fig. 4B*), the first one armed with spinules, apically with 6 elements: 1 unipinnate spine and 1 longer unipinnate seta, plus 3 long geniculate setae (one broken in Fig. 4B), the outermost fused to a tiny bare seta (broken in Fig. 4B).

Md (Fig. 5A) produced into long gnathobase that ends in 2 strong and bicuspidate teeth and 1 less strong element that ends in four fine tips; apart from that, the gnathobase lacks any ornamentation. Mandibular palp 1-segmented, with 1 basal (Fig. 5A: seta no. 2), 1 exopodal (6),

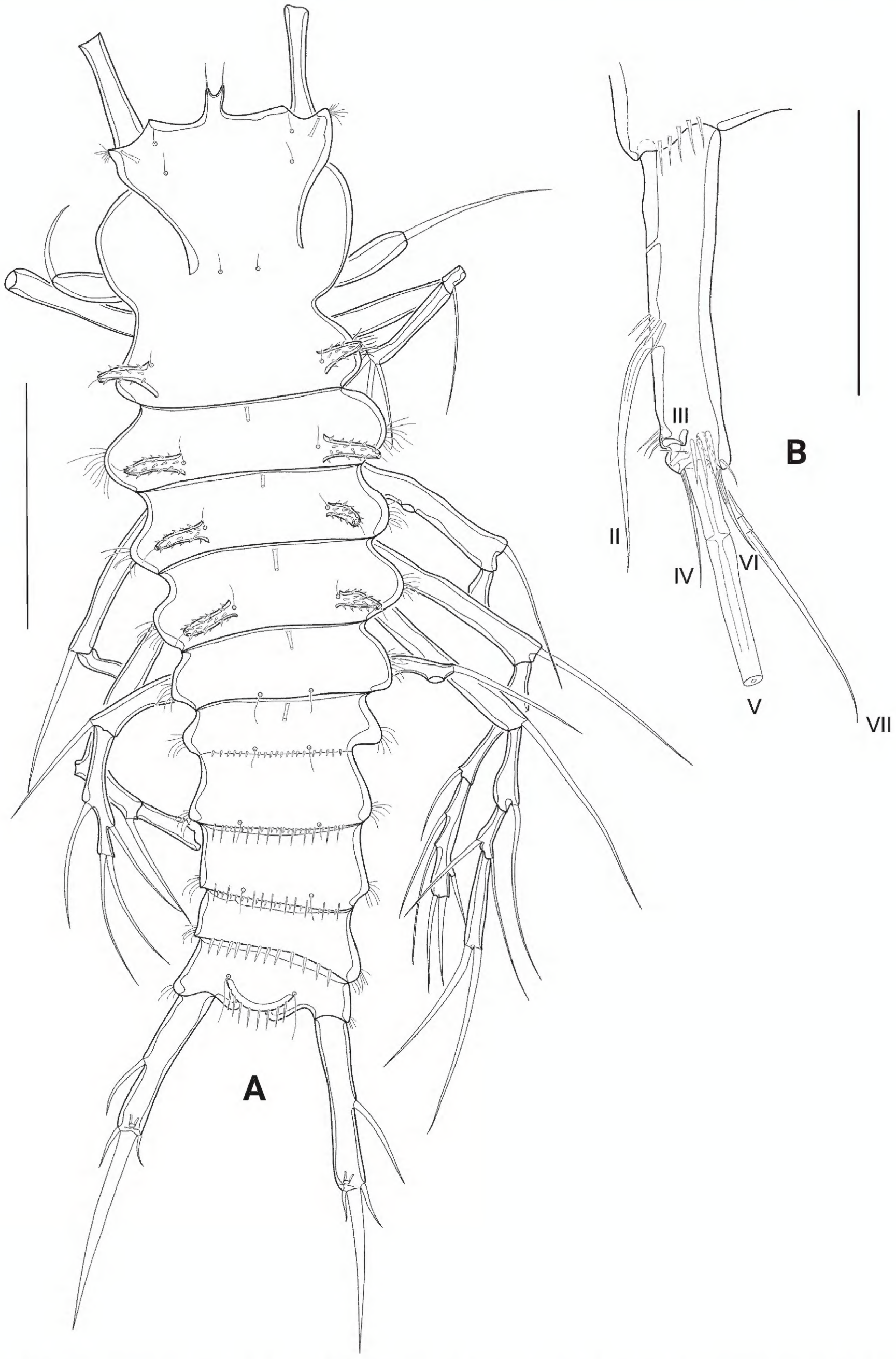

Figure 3. *Dorsiceratus karinae* sp. nov.; **A.** Holotype, female, Eratosthenes Seamount, station #1100/1-4. Habitus, dorsal view; **B.** Paratype 4, female, Eratosthenes Seamount, station #1095/6-10. Right FR, ventral view, with numbered furcal setae. Scale bars: 100 μm (**A**); 50 μm (**B**).

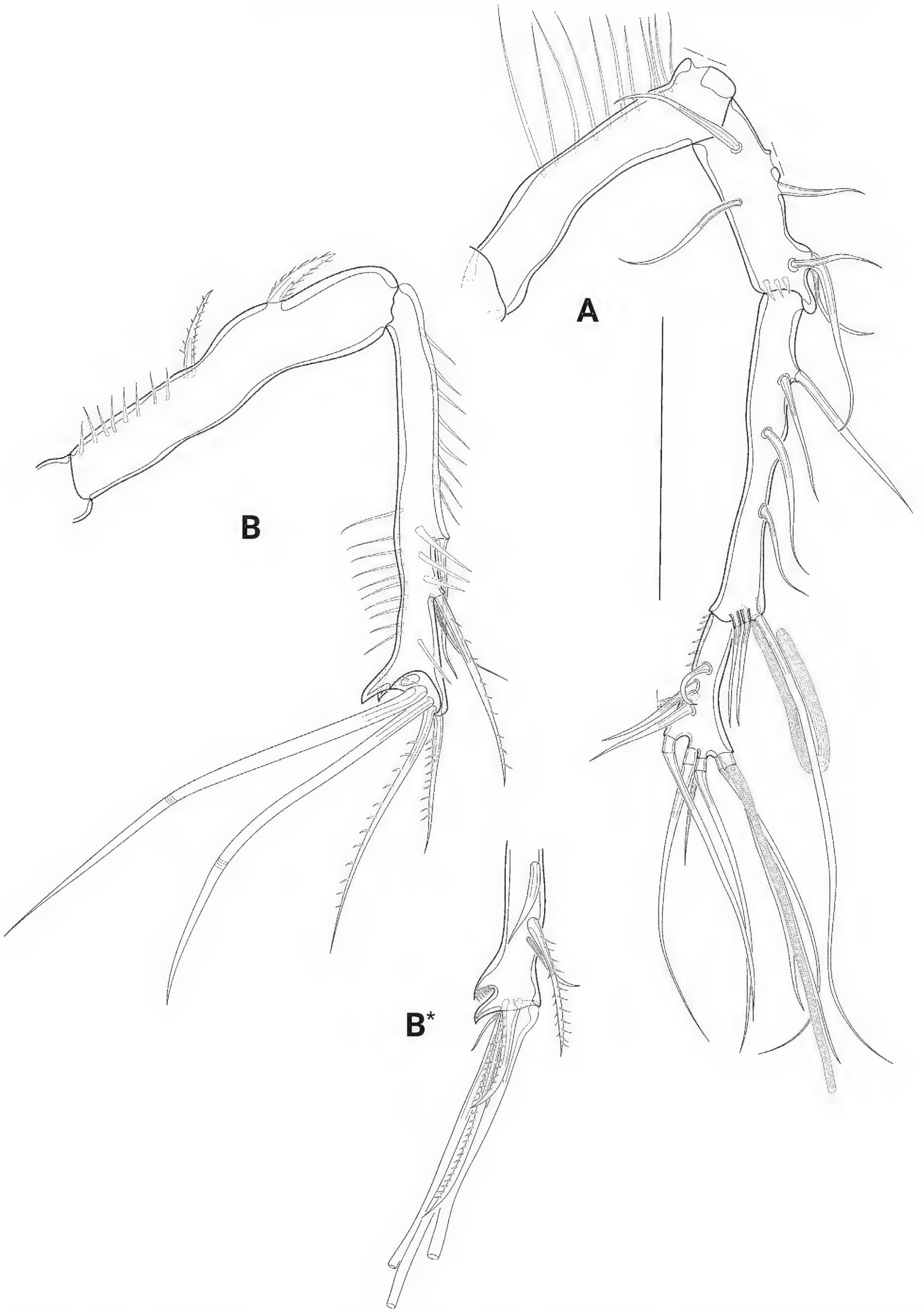

Figure 4. *Dorsiceratus karinae* sp. nov., holotype, female, Eratosthenes Seamount, station #1100/1-4. **A.** A1; **B.** A2; **B*.** Apical part of the A2 endopod, shown from the counterpart. Scale bar: 50 µm.

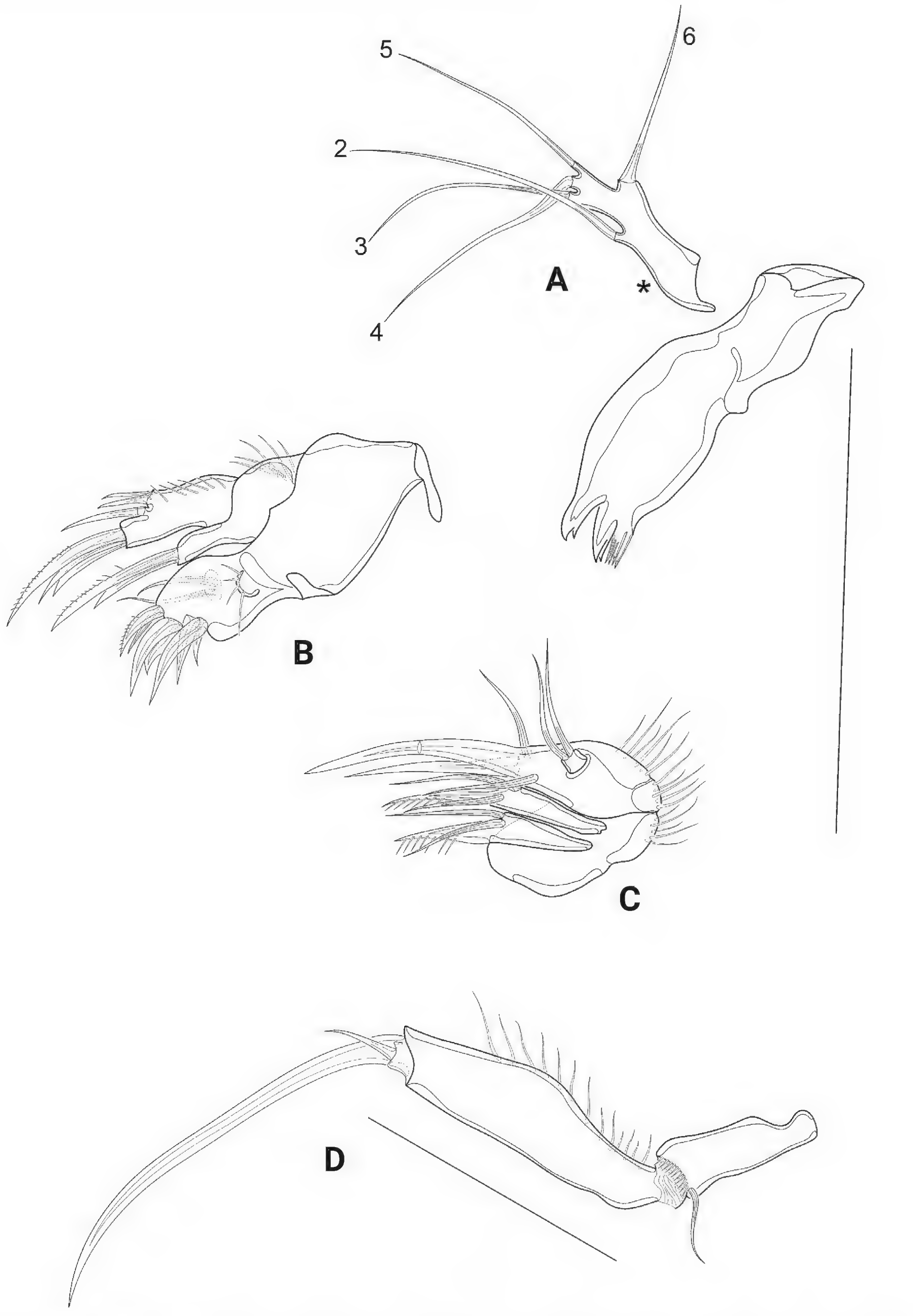

Figure 5. *Dorsiceratus karinae* sp. nov., **A.** Paratype 7, female, Eratosthenes Seamount, station #1112/7-1. Md, with md palpus separated and numbered setae; asterisk * indicating former position of lost basal seta no. 1; **B.** Paratype 7, female, Eratosthenes Seamount, station #1095/6-12. Mxl; **C.** Paratype 5, female, Eratosthenes Seamount, station #1112/7-1. Mx; **D.** Holotype, female, Eratosthenes Seamount, station #1100/1-4. Mxp. Scale bar: 50 µm.

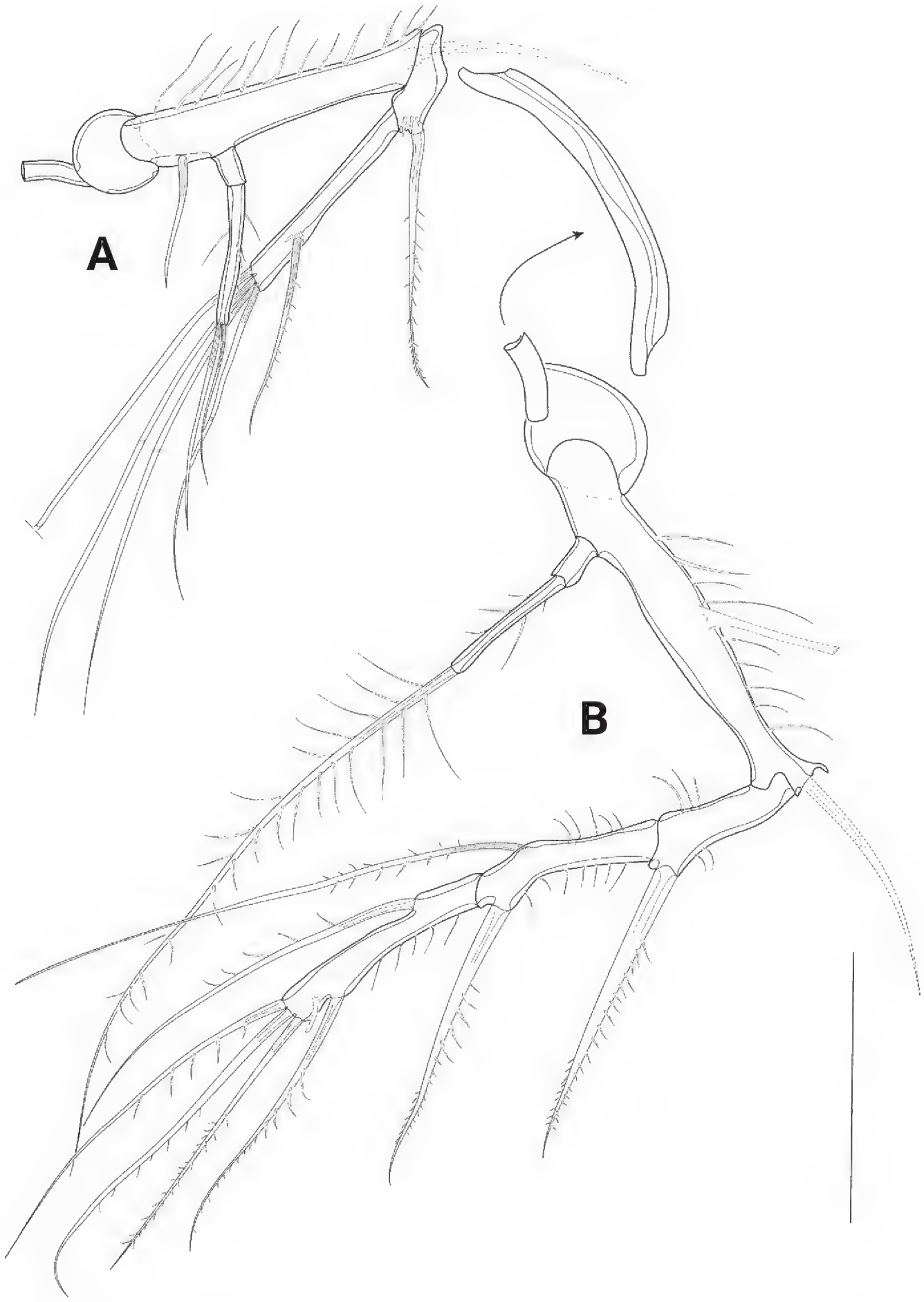

Figure 6. *Dorsiceratus karinae* sp. nov., Holotype, female, Eratosthenes Seamount, station #1100/1-4. **A.** P1; **B.** P2, intercoxal sclerite separate. Scale bar: 50 µm.

and 3 endopodal setae (3–5); basal seta no. 1 completely reduced (Fig. 5A: asterisk*).

Mxl (Fig. 5B) with praecoxal arthrite bearing 7 strong apical spines, one of which unipinnate, and 2 surface setae. Coxa basally with few long spinules and apically with 1 unipinnate and 1 bare seta. Basis, endo- and exopod fused, carrying 3 lateral setae and 3 apical spines, one of which unipinnate.

Mx (Fig. 5C) syncoxa with 2 endites and few long spinules along distal margin. Both endites of similar shape, not fused to syncoxa, and carrying each 2 bare setae and 1 strong unipinnate spine fused with the segment. Allobasis distinct, also with long spinules at distal margin and produced into strong bare claw; additionally, with 2 bare setae and 1 bare spine. Endopod small and knob-like, equipped with 2 bare setae.

Mxp (Fig. 5D) slender; syncoxa apically with row of spinules and 1 bare seta; basis about 1.6 times longer than syncoxa, with row of long spinules at outer margin; endopod produced into bare, lean claw longer than basis and accompanied by 1 tiny seta at its base.

P1–P4 with transversely elongated bases that present a row of long spinules at their anterior margins and 1 outer seta (broken in all corresponding figures); P2–P4 bases additionally with long tube pore. Intercoxal sclerites (exemplified by that from the P2) long and bow-like. Endopods 2-segmented (except male P3 endopod; see below), exopods P2–P4 3-segmented.

P1 (Fig. 6A) basis additionally with 1 bare inner seta; enp1 without setae or spinules, enp2 with few long spinules at inner and outer margins and with 2 apical bare setae, the inner one being slightly longer than the outer

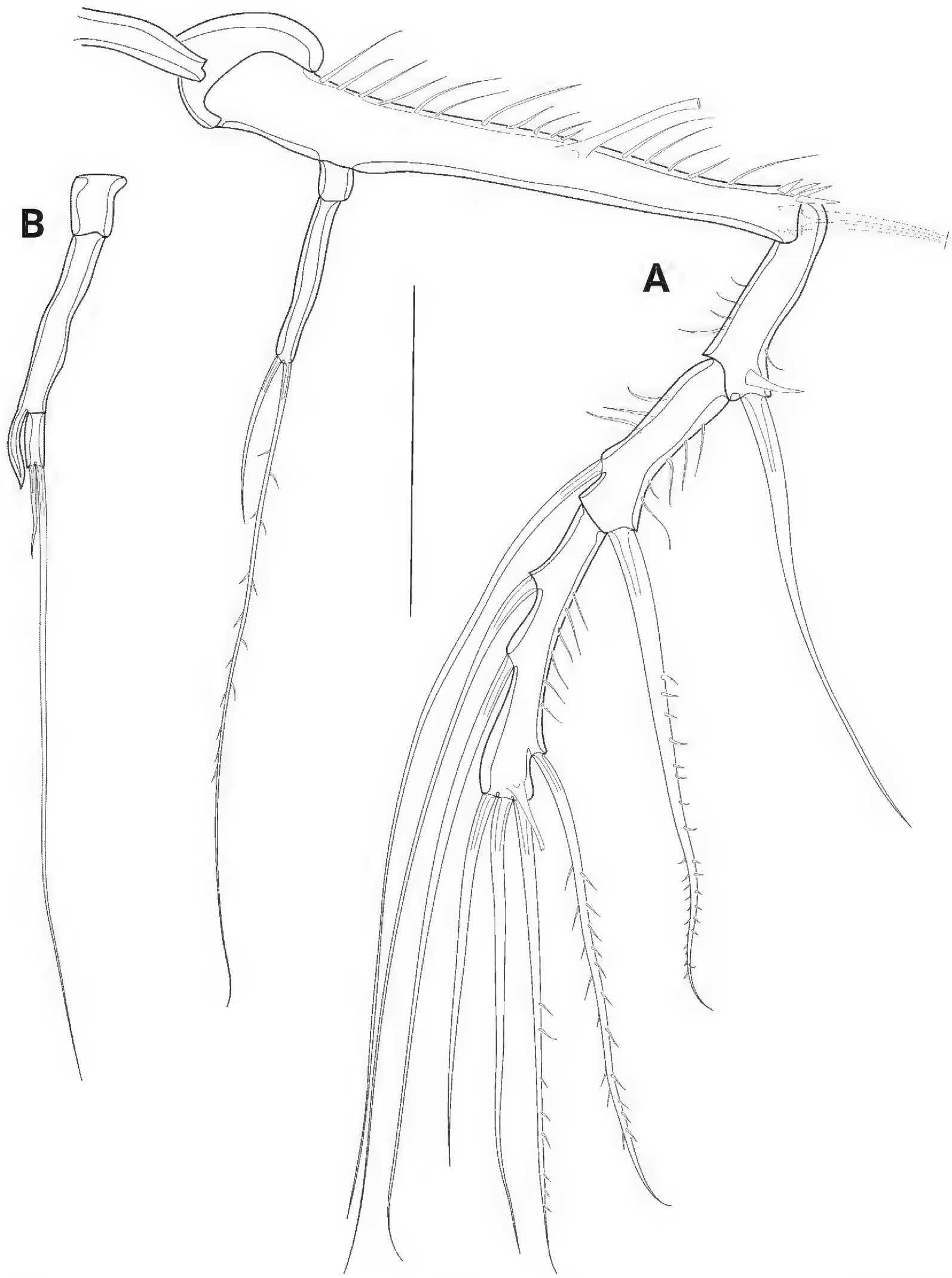

Figure 7. *Dorsiceratus karinae* sp. nov., **A.** Holotype, female, Eratosthenes Seamount, station #1100/1-4. P3; **B.** Paratype 1 (allotype), male, Eratosthenes Seamount, station #1112/8-3. P3 endopod. Scale bar: 50 µm.

one. Exopod 2-segmented, exp1 carrying 1 long bipinnate outer seta; exp2 more than 2 times longer than exp1, outer unipinnate seta arising at distal third, 4 geniculate bare setae inserting apically.

P2–P4 (Figs 6B, 7A, 8A) with enp1 being unarmed and much shorter than enp2; P2 enp2 (Fig. 6B) with some spinules at inner and outer margins and 1 biplumose apical seta that exceeds the length of the whole exopod. P3 and P4 endopods (Figs 7A, 8A) without spinules but bearing 2 apical setae: the inner one short and bare, the outer one bipinnate and about 4 times longer than the inner one in the P3 (Fig. 7A), whilst biplumose and nearly 5 times longer than the inner one in the P4 (Fig. 8A). Exopods with slender segments of increasing length from exp1 to exp3. All segments except P4 exp3 with rows of spinules at inner and/or outer margin; exp1 with long outer seta, exp2 with 1 outer and 1 inner seta, the latter bipinnate (P2), bare (P3), or biplumose (P4). Exp3 as depicted with 2 uni- or bipinnate outer setae, as well as with 2 apical setae (unipinnate in P2, bare in P3, and biplumose in P4); P2 and P4 additionally with 1 inner seta (uniplumose in P2, biplumose

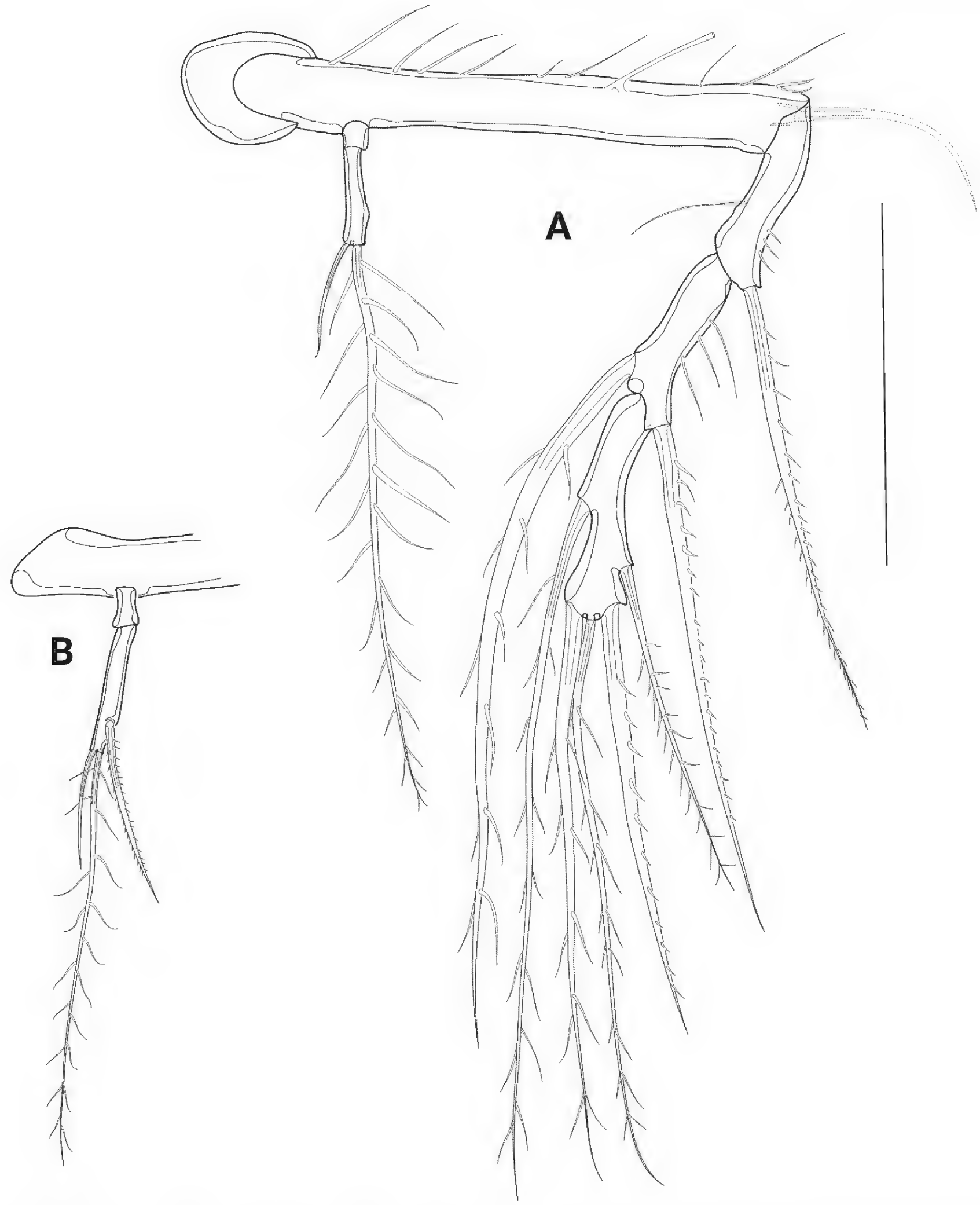

Figure 8. *Dorsiceratus karinae* sp. nov., **A.** Holotype, female, Eratosthenes Seamount, station #1100/1-4. P4; **B.** Paratype 1 (allotype), male, Eratosthenes Seamount, station #1112/8-3. P4 endopod. Scale bar: 50 µm.

in P4), P3 with 2 bare inner setae. P2 and P3 with long tube pore located between the outer elements. Setation of P1–P4 as given in Table 3.

P5 (Fig. 9A) with slender basoendopod that bears a row of long spinules along anterior margin and a long bare outer seta arising from short, square setophore and accompanied by long tube pore; endopodal lobe completely incorporated into basis, with 2 bare setae and 1 tube pore. Exopod long and slender, approximately 1.5 times longer than basoendopod, with 1 outer unipinnate and 1 inner bare seta, 1 bare subapical seta shifted to the posterior surface, and 2 apical bipinnate setae.

Table 3. *Dorsiceratus karinae* sp. nov., setation of swimming legs P1–P4. Roman numerals indicate outer setae/spines.

	Exopod	Endopod
P1	0-1; 0-2-III	0; 0-2-0
P2	0-1; 1-1; 1-2-II+tube pore	0; 0-1-0
P3	0-1; 1-1; 2-2-II+tube pore	0; 0-2-0
P4	0-1; 1-1; 1-2-II	0; 0-2-0

P6 and GF (Fig. 9B). P6 small, lobes fused to a narrow clasp-like structure that carries 1 bare seta on each outer side; close to the gonopore, that "clasp" bulges out slightly, being strengthened by a pair of sclerotised "ribs".

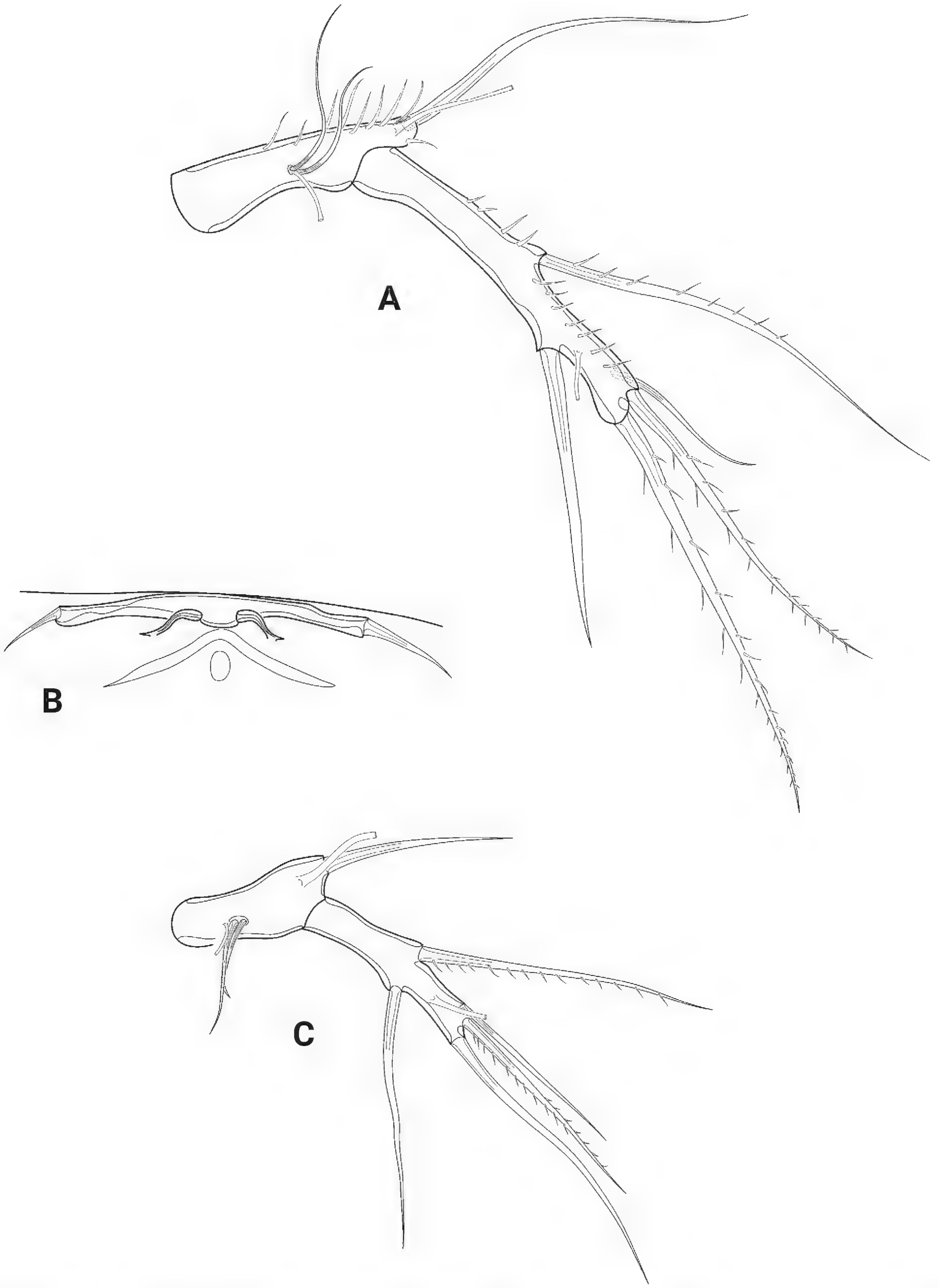

Figure 9. *Dorsiceratus karinae* sp. nov., **A.** Holotype, female, Eratosthenes Seamount, station #1100/1-4. P5; **B.** Holotype, female, Eratosthenes Seamount, station #1100/1-4. genital field; **C.** Paratype 1 (allotype), male, Eratosthenes Seamount, station #1112/8-3. P5. Scale bar: 50 µm.

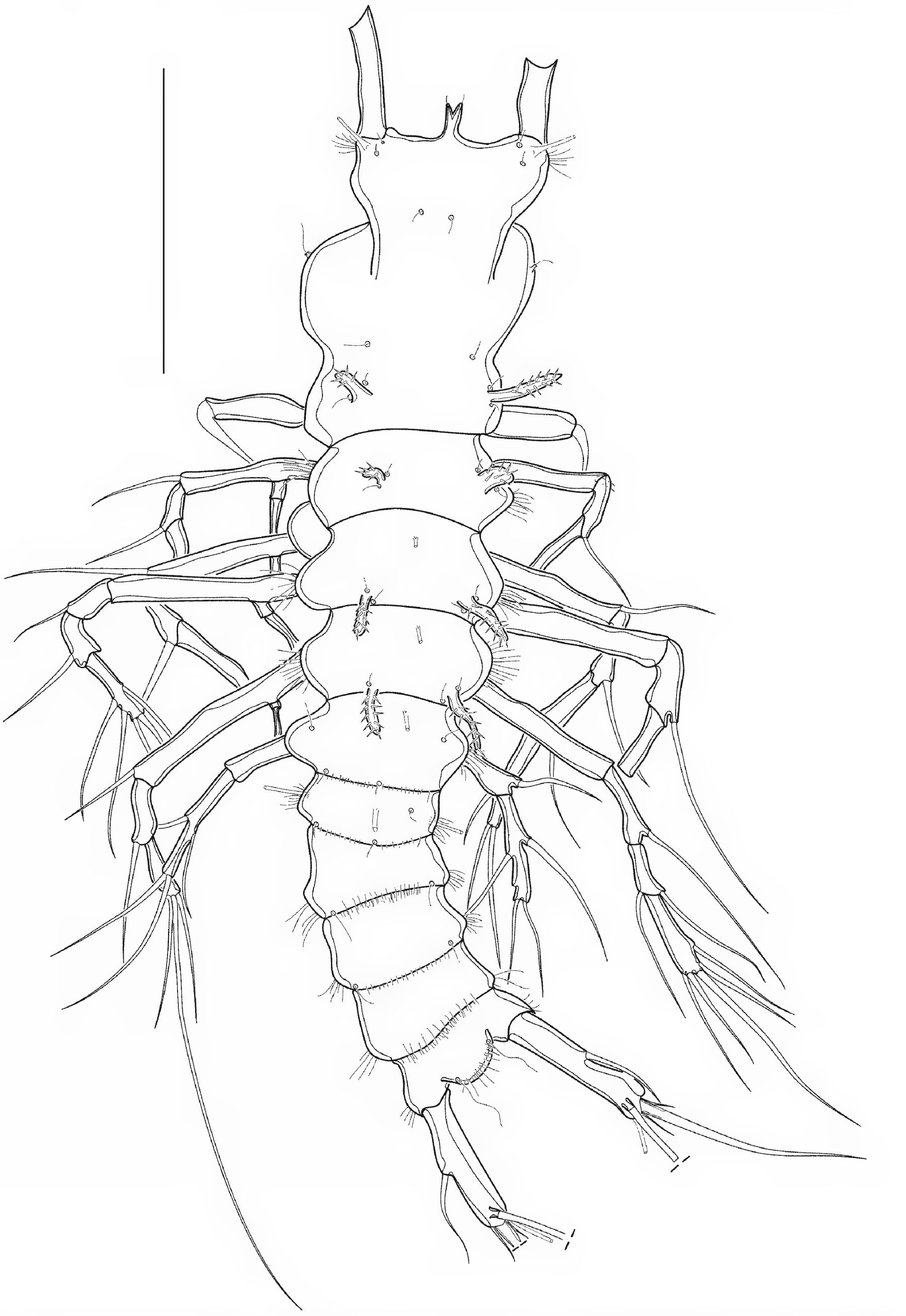

Figure 10. *Dorsiceratus karinae* sp. nov., paratype 1 (allotype), male, Eratosthenes Seamount, station #1112/8-3. Habitus, dorsal view. Scale bar: 100 µm.

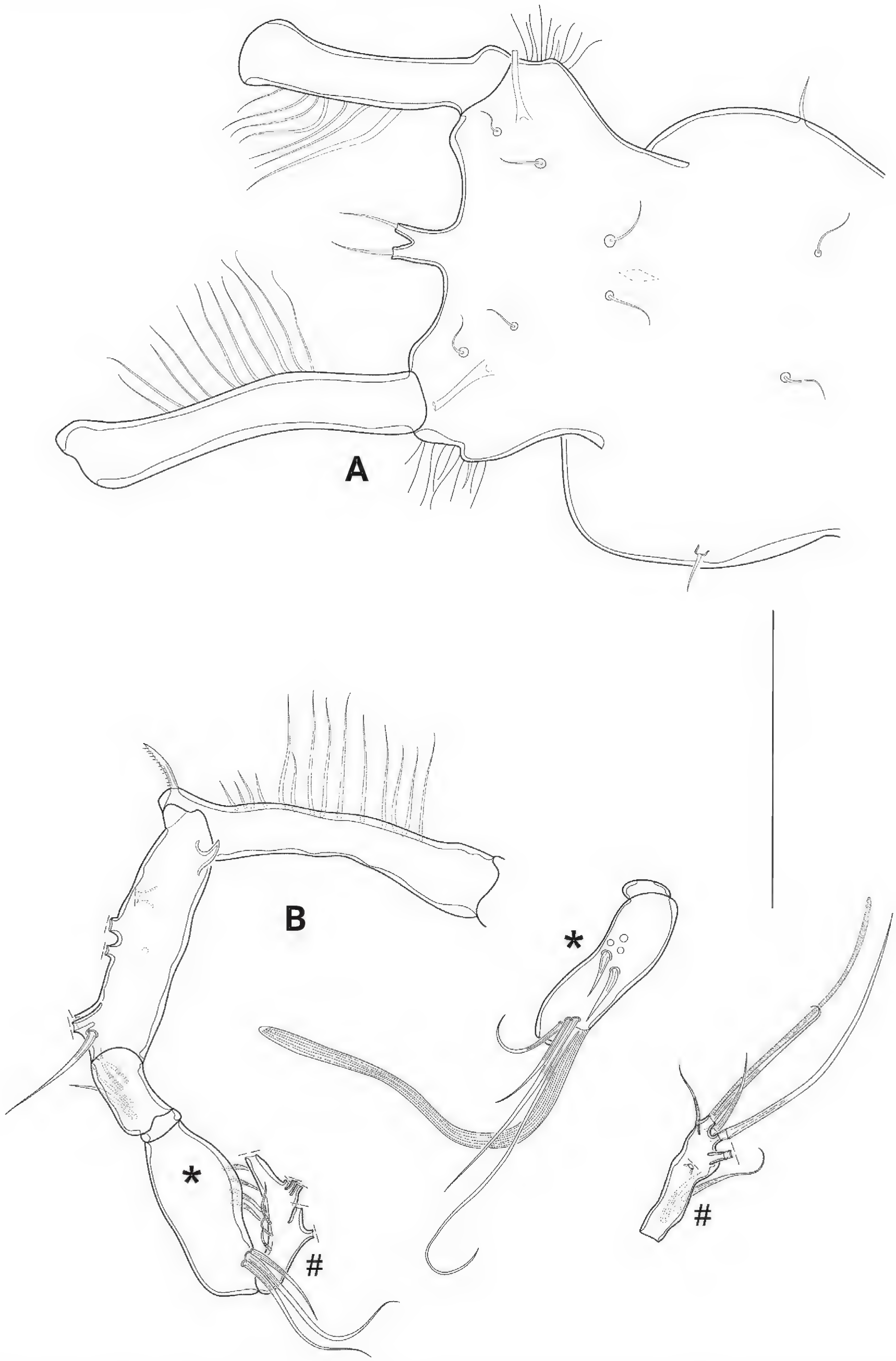

Figure 11. *Dorsiceratus karinae* sp. nov., paratype 1 (allotype), male, Eratosthenes Seamount, station #1112/8-3. **A.** Cephalothoracic peak with rostrum, dorsal view; **B.** A1, * and # showing fifth and sixth segments from counterpart. Scale bar: 50 μm.

Description of male. Male resembling female in most aspects, except in the shape of the A1, P3, and P4 endopods and P5.

Habitus (Fig. 10) as in female but smaller, slenderer, and lacking GDS. Body length from rostral tip of PT 6 to end of FR 376 µm (mean: 374 µm, range: 352–401 µm, n = 4). Rostrum (Fig. 11A) fused with cphth, strongly constricted, slightly longer than broad, and cleft at its tip, with 2 sensilla; tube pore not recognisable in any of the four males.

A1 (Fig. 11B) consisting of 6 segments, chirocer, geniculation between fifth and sixth segments. The first two segments longest, the third and sixth segments slightly shorter than the fifth one, which is slightly swollen; acrothek not discernible; the fourth segment minute, unarmoured. Setal formula: I–1; II–7; III–4; IV–0; V–9 + aes; VI–9 + aes.

P3 exopod as in female. Endopod 3-segmented (Fig. 7B), enp1 tiny and bare, enp2 more than three times longer than enp1, ending on inner apical edge in cuspidal apophysis that slightly overtops the apical margin of enp3. The latter is as long as enp1 and bears 2 apical bare setae, the outer one being approximately seven times longer than the inner one.

P4 exopod as in female. Endopod 2-segmented (Fig. 8B), enp1 small, nearly squarish, and bare. Enp2 about 3.4 times longer than enp1, apically with 2 setae, the inner one bare, the outer one approximately 3.4 times longer than the inner seta and biplumose. Subapically on the outer margin arises 1 bipinnate spine.

P5 (Fig. 9C) generally as in female but smaller. Basoendopod more compact than that of female, without spinulose row; endopodal area with 2 bare setae and small tube pore. Exopod only slightly longer than basoendopod, without spinulose ornamentation, setation as in female, likewise with 1 tube pore.

Dorsiceratus denizae sp. nov.

https://zoobank.org/F712FEC9-9649-4A75-BC84-7DA6B8625EBF

Figs 12–15

Locus typicus. Angola Basin, station #346/5-9, geographic position 16°16.9'S, 05°27.0'E, depth 5,389 m, tropical southeast Atlantic Ocean.

Type material. The type material was collected during research cruise M48/1, expedition DIVA 1, of RV METEOR.

• Holotype: female, collected on 27.07.2000 at the type locality; mounted on 1 slide, collection number SMF 37292/1; • PT1: female, collected on 27.07.2000 at station #346/8-1 (AB_C), geographic position 16°17,0'S, 05°27,0'E, depth 5,390 m; mounted on 1 slide, collection number SMF 37293/1;• PT2: female, collected on 14.07.2000 at station #325/7-4 (AB_S), geographic position 19°58,4'S, 02°59,8'E, depth 5,448 m; mounted on 1 slide, collection number SMF 37294/1.

Etymology. The epitheton of *Dorsiceratus denizae* sp. nov. is fondly dedicated to SY's daughter, Miss Deniz Yurtdaş. Gender: feminine.

Description of female. Habitus (Fig. 12) slender and cylindrical, with inconspicuous boundary between pro- and urosome. Body length of holotype from rostral tip to end of FR 686 µm (mean 717 µm, range: 686–747 µm, n = 3), cphth and body somites dorsally with some sensilla and tube pores. Frontal peak on cphth well-developed, with anterior cephalothoracic setular tufts (ACST). Cphth and first three free thoracic somites dorsally with slender spinulose cuticular processes (CLDP, DT1–DT3), that bear a sensillum at their tips and are accompanied by another sensillum at their bases. Rostrum fused with cphth, strongly constricted, slightly longer than broad and cleft at its tip, with 2 sensilla and 1 tube pore. Last thoracic and first abdominal somite fused into a GDS; former segmental demarcation still indicated by few dorsal spinules and pair of sensilla. Free thoracic body somites laterally with setular tufts.

P2–P6-bearing somites dorsally with 1 tube pore. First abdominal somite (= posterior half of GDS) and the following two abdominal somites dorsally with row of flexible setules on posterior margin; first and second abdominal somites additionally with 2 pairs of sensilla. Penultimate somite dorsally with tube pore on posterior margin. Telson shorter than broad, slightly trapezoidal from dorsal view. Anal operculum basally flanked by a pair of sensilla; apically with long spinules, which increase in length from the outer edges towards the centre.

FR (Fig. 13A) approximately 7 times longer than basal width, slender, equipped with 7 setae. Setae I and II located at mid-length of ramus; seta I minute, bare; seta II much longer, bipinnate; seta III (broken in Fig. 13A) arising subapically; setae IV and VI small and bare, inserting apically on outer and inner edges, respectively; seta V longest; seta VII (broken in Fig. 13A) positioned dorsally at subapical part of FR. FR additionally with 1 short broad and 1 slender tube pore on the ventral apical margin.

A1 (Fig. 13B) 4-segmented. First segment longest, with long spinules on anterior margin, distally with 1 biplumose seta. Second segment reaching 2/3 of first segment, with 6 setae. Third segment almost as long as first, with row of spinules on posterior margin and with 3 bare and 1 bipinnate setae along anterior margin; moreover, subapically, 1 seta and 1 strong aes arise from acrothek, accompanied by 2 bare setae. Fourth segment smallest, with 10 setae (4 of which broken) and 1 aes. Setal formula: I–1, II–6, III–7 + aes, IV–10 + aes.

A2, md, mxl, and mx as in *Do. karinae* sp. nov.

Mxp (Fig. 14A) syncoxa slender, apically with crest of spinules and 1 uniplumose seta; basis about 1.8 times longer than syncoxa, carrying some long fine spinules along outer margin; endopod produced into lean claw longer than basis, unipinnate at its distal half and accompanied by 1 short bare seta at its base.

P1–P4 with transversely elongated bases that present a row of long fine spinules on their anterior margins and 1 outer seta; P2–P4 bases additionally with long tube pore.

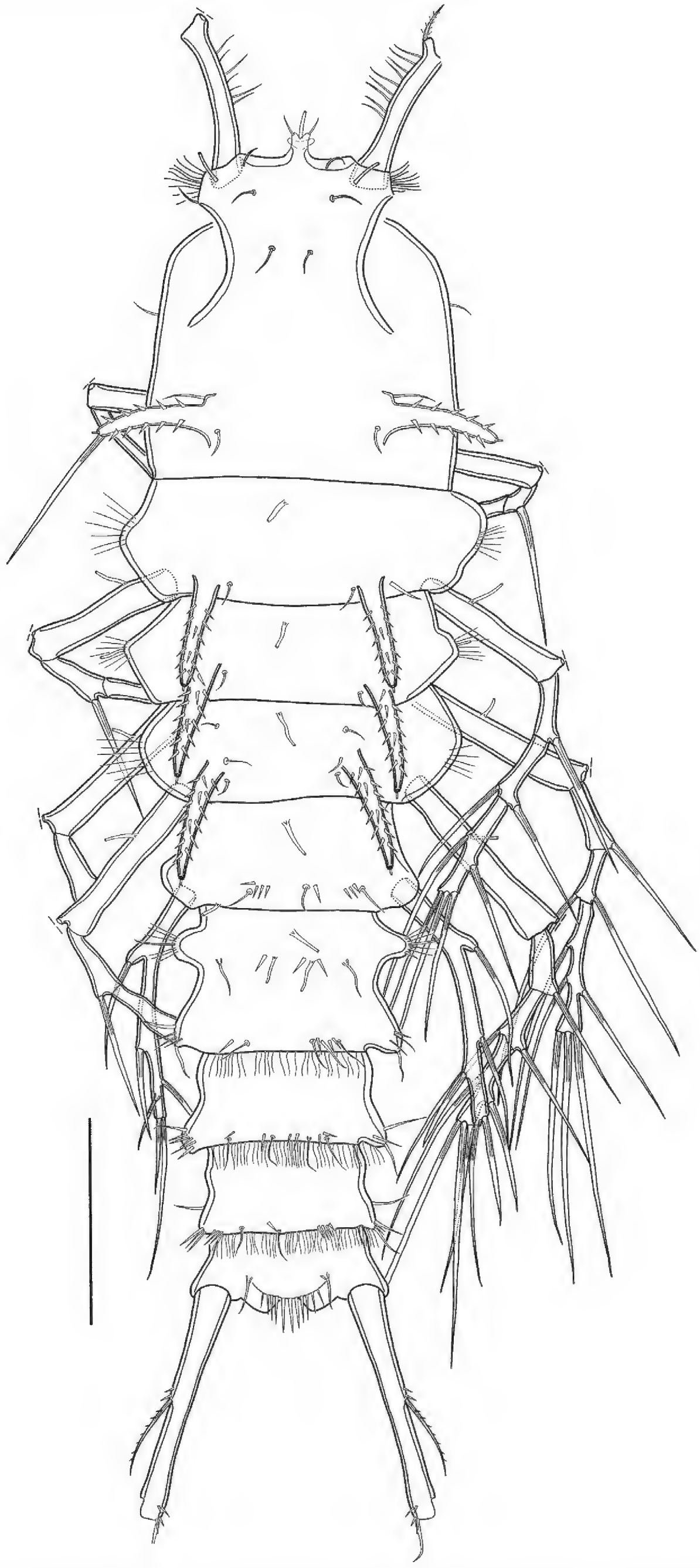

Figure 12. *Dorsiceratus denizae* sp. nov., holotype, female, Central Angola Basin, station #346/5-9. Habitus, dorsal view. Scale bar: 100 µm.

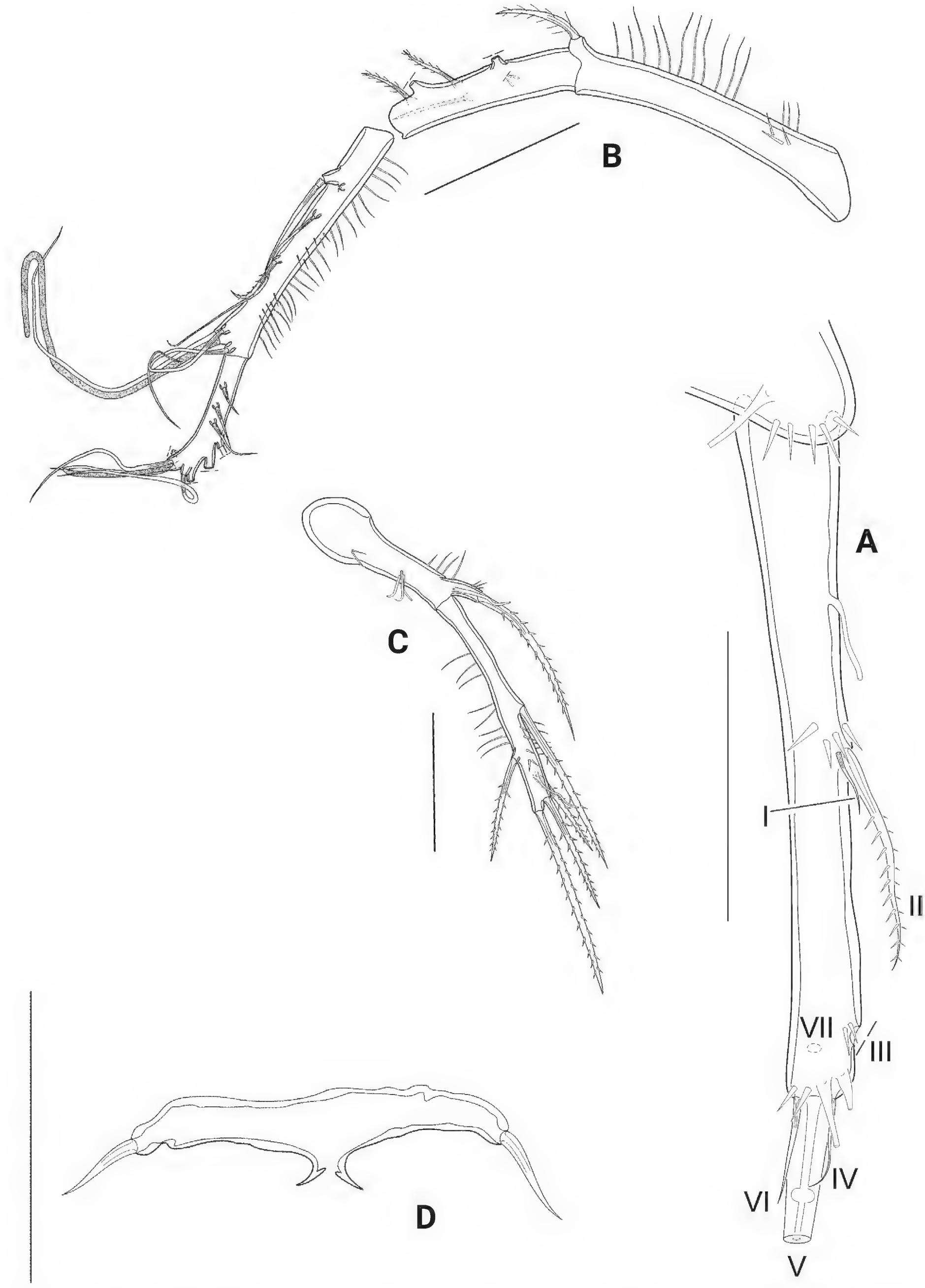

Figure 13. *Dorsiceratus denizae* sp. nov., holotype, female, Central Angola Basin, station #346/5-9. **A.** Left FR, ventral view, with numbered setae; **B.** Female A1 (broken between second and third segment); **C.** Female P5; **D.** Female P6 with genital field. Scale bars: 50 µm.

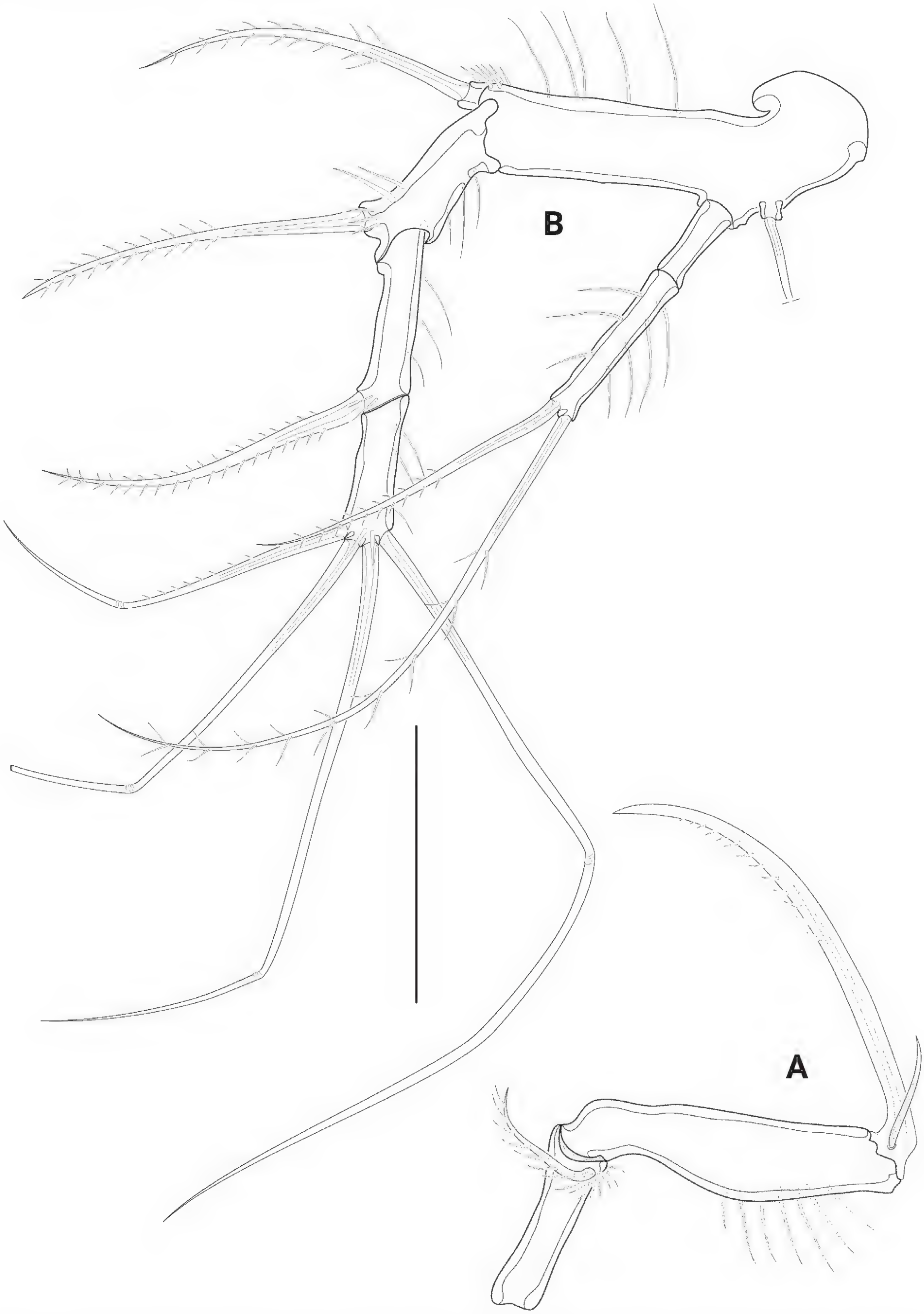

Figure 14. *Dorsiceratus denizae* sp. nov., holotype, female, Central Angola Basin, station #346/5-9. **A.** Mxp; **B.** P1. Scale bar: 50 μm.

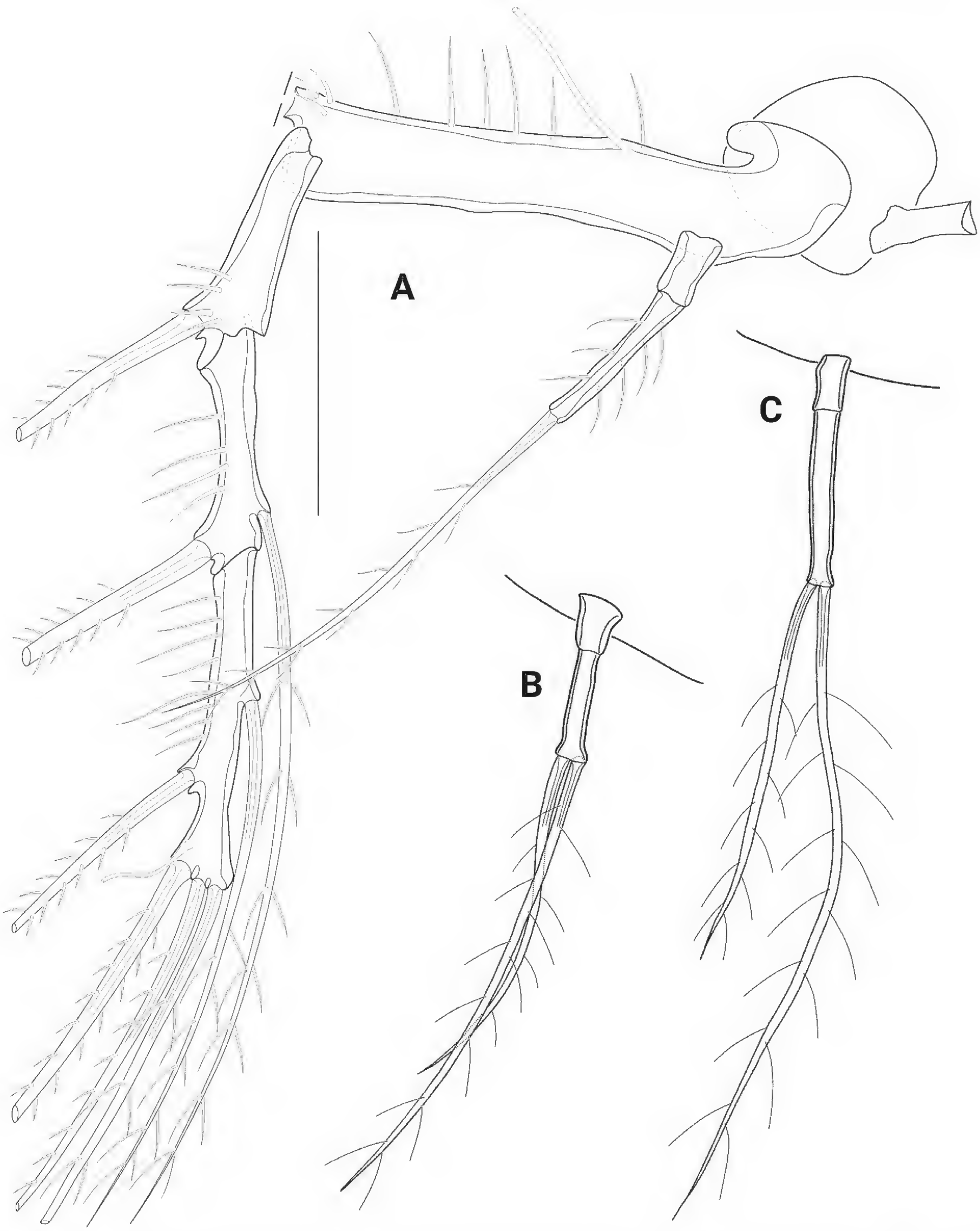

Figure 15. *Dorsiceratus denizae* sp. nov., holotype, female, Central Angola Basin, station #346/5-9. **A.** P2; **B.** Female P3 endopod; **C.** Female P4 endopod. The internal endopodal side is that of the shorter (= inner) apical seta. Scale bar: 50 µm.

Intercoxal sclerites long and bow-like, as in *Do. karinae* sp. nov. Endopods 2-segmented, exopods 3-segmented.

P1 (Fig. 14B) basis additionally with 1 bare inner seta (broken in Fig. 14B); enp1 smaller than enp2, without setae or spinules; enp2 with few long spinules on inner and outer margins and with 2 apical setae, the inner one biplumose and longer than the outer bipinnate one. Exp1 with few spinules on outer and inner margin and with 1 long bipinnate outer seta; exp2 longest, with fine spinules on inner margin and 1 outer bipinnate seta; exp3 as long as exp1, carrying 4 geniculate setae apically, outermost seta unipinnate until geniculation.

P2–P4 (Fig. 15A–C). P2 (Fig. 15A) enp1 short, without ornamentation; enp2 about 2.4 times longer than

enp1, with long fine spinules along inner and outer margin, apically with 1 long biplumose seta; exp1 with few spinules on distal outer edge, and with 1 long bipinnate outer seta; exp2 as long as exp1, with spinules along outer margin, and with 1 slender biplumose inner and 1 bipinnate outer seta; exp3 about 1.5 times longer than previous segments, with long fine spinules and 2 bipinnate setae along outer margin, the distalmost arising apically, accompanied by long tube pore; additionally with 2 apical setae, the outermost unipinnate, the innermost biplumose, and with 1 biplumose inner seta. Shape of bases and exopods of P3 and P4 (not drawn) as for P2; P3 exp3 of PT1 with tube pore. P3 and P4 enp1 small, unarmoured; P3 enp2 (Fig. 15B) about twice as long as enp1, lacking spinules but apically equipped with 2 biplumose setae, the innermost shorter than the outermost; P4 enp2 (Fig. 15C) also without spinules, enp2 2.8 times longer than enp1, setation as for P3 enp2. Setal formula given in Table 4.

Table 4. *Dorsiceratus denizae* sp. nov., setation of swimming legs P1–P4. Roman numerals indicate outer setae.

	Exopod	Endopod
P1	0-1; 0-1; 0-2-II	0; 0-2-0
P2	0-1; 1-1; 1-2-II+tube pore	0; 0-1-0
P3	0-1; 1-1; 2-2-II	0; 0-2-0
P4	0-1; 1-1; 1-2-II	0; 0-2-0

P5 (Fig. 13C). Basoendopod and exopod distinct. Basoendopodal outer seta arising from short setophore accompanied by long tube pore and few spinules; endopodal lobe completely incorporated into basal part, represented by 1 tiny bare seta and 2 tube pores. Exopodal lobe slender, longer than basoendopodal part, with spinulose row on inner margin and equipped with 1 outer and 1 inner bipinnate seta each; apically with 2 bipinnate setae, subapically with 1 tube pore, and on the posterior surface with 1 bipinnate seta.

P6 (Fig. 13D) small, forming single plate and bearing 1 small bare seta on left and right margins. Genital field not clearly discernible, indicated by paired cuticular clasps on posterior margin of P6 plate.

Male unknown.

Remarks: *Dorsiceratus denizae* sp. nov. is characterised above all by its body size and the particularly long furcal rami (l/w ratio = 7). Another common character of the four individuals is the possession of only 1 seta on the P5 basoendopod. This constellation is also found in two other specimens from the Angola Basin (Table 2: *Do.* 18 and *Do.* 23) (and in *Do. octocornis*), but *Do. denizae* sp. nov. is much larger than the latter and has much longer FR.

Dorsiceratus andeep sp. nov.

https://zoobank.org/393DE4DF-9846-4C2C-9C70-58E2D78DC3A2

Figs 16–18

Locus typicus. east of the Antarctic Peninsula, western Weddell Sea, Antarctica, station #133/8-C (65°20,09'S, 54°14,72'W, 1108.0 m water depth).

Type material. ***Holotype*:** female, collected on 07.03.2002, put on one slide, collection number SMF-37295/1.

Etymology. the epitheton *andeep* refers to the Expeditions ANtarctic benthic DEEP-sea biodiversity (ANDEEP) I + II of RV POLARSTERN (cruise PS61) that had taken place in 2002 to the Scotia Arc, the Weddell Sea, and the Antarctic peninsula.

Description of female. The body shape (not drawn) corresponds to the generic diagnosis with the pronounced frontal peak, the formation of cuticular processes on the cphth and the first three free thoracic segments, as well as the structure of the extremities. With a body length of 799 µm, *Do. andeep* sp. nov. is, however, the largest described representative of the genus *Dorsiceratus* to date. Rostrum (Fig. 16A) constricted, about 1.6 times longer than broad, cleft at its tip and bearing 2 sensilla and 1 long tube pore.

FR (Fig. 17A) about seven times as long as wide, bearing 7 setae: setae I and II insert on the outer margin halfway along the FR; seta I is tiny and bare, with the bipinnate seta II located right next to it; seta III is bare and inserts subapically on the outer side; seta V is the longest, located apically and flanked externally by seta IV and internally by seta VI, both of which are small and bare; seta VII is biarticulated and arises subapically on the dorsal side of the FR.

A1 (Fig. 16B) 4-segmented, segments 1–3 of about equal length, segment 4 only about half as long as the preceding ones. First segment anteriorly with a row of long spinules. All setae bare. Setal formula: I–1; II–6; III–6 + aes; IV–9 + aes.

A2 and mouthparts as in *Do. karinae* sp. nov.

P1 (Fig. 17B) with transversely broadened base, 2-segmented endopod, and 3-segmented exopod. Enp1 about half as long as enp2, without spinules; enp2 also naked, apically with 2 naked setae, the outer one about 1/3 longer than the inner one. Exp1 with 1 bipinnate outer seta; only 1 spinule recognisable on the outer margin; exp2 slightly longer than exp1, without spinules and also with 1 bipinnate outer seta; exp3 shortest, without spinules and tubular pore, but with 4 bare geniculate apical setae.

P2–P4 (Fig. 18A–C) of almost identical shape, with bow-shaped intercoxal sclerites, transversely broadened bases, 2-segmented endopods, and 3-segmented exopods (exemplified by P2, Fig. 18A). Bases without long spinules, but with tube pore on anterior margin. Number of setae on endo- and exopods as listed in Table 5. P2–P4 exp3 (Fig. 18A, B, C, respectively) lacking inner setae; P2 and P3 exp3 (Fig. 18A, B) bear a tube pore.

P5 (Fig. 16C) with basoendopod and exopod separated; outer seta of basoendopod arises from a setophore accompanied by a tube pore; endopodal part completely reduced and represented only by 2 bare setae but no tube pores; exopod longer than basoendopod, with 5 bipinnate setae; seta II displaced to posterior surface. In addition, a tube pore is located anteriorly.

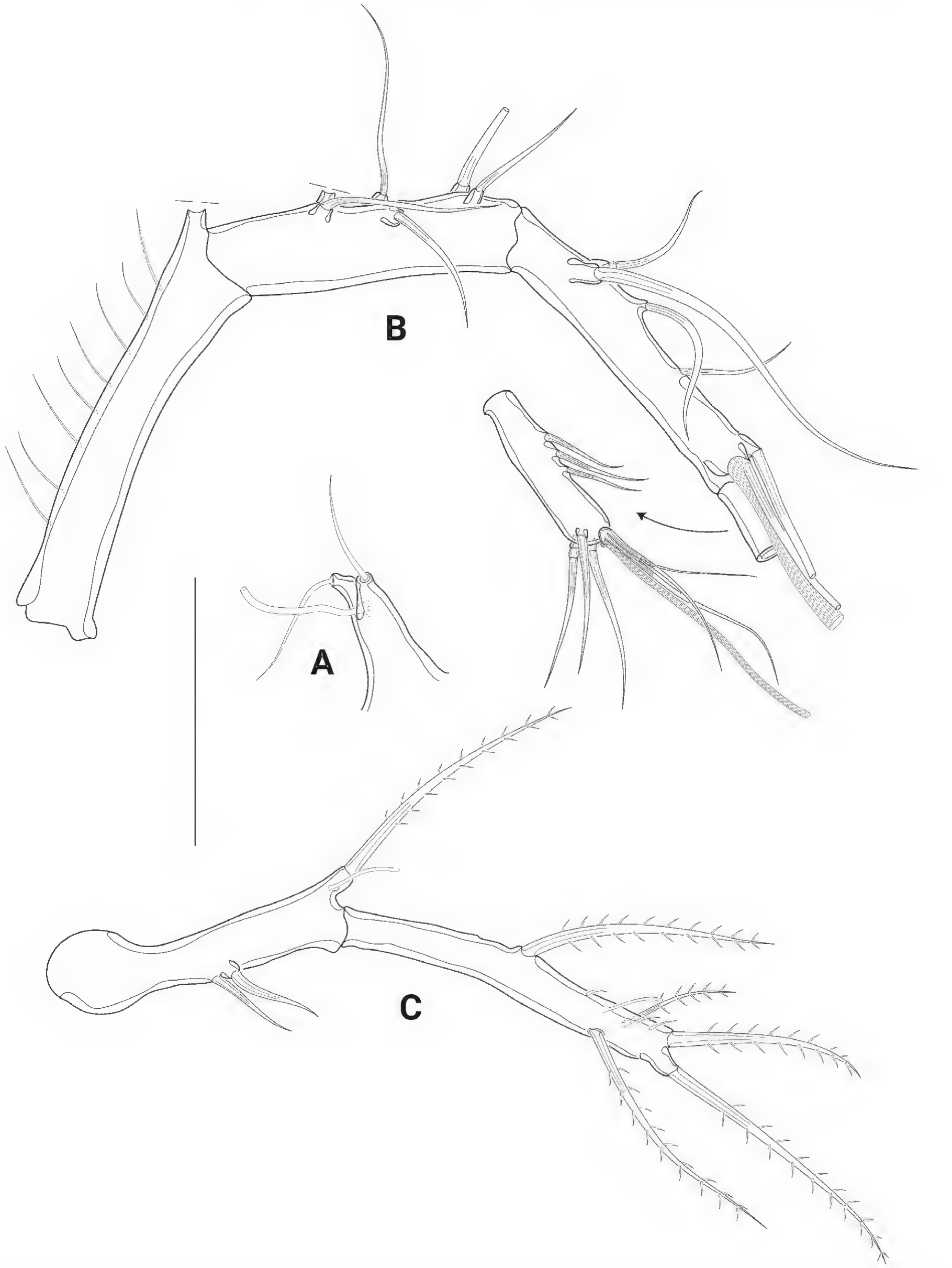

Figure 16. *Dorsiceratus andeep* sp. nov., holotype, female, east of Antarctic Peninsula, station #133/8-C. **A.** Rostrum, view of ¾ front; **B.** Female A1, terminal segment drawn separately; **C.** Female P5. Scale bar: 50 µm.

Due to the dense coverage of the individual with detritus, the P6 and the GF were not described.

Male unknown.

Remarks. It is noteworthy that of the four *Dorsiceratus* specimens found at the same Antarctic station, only the female could be distinguished from the three

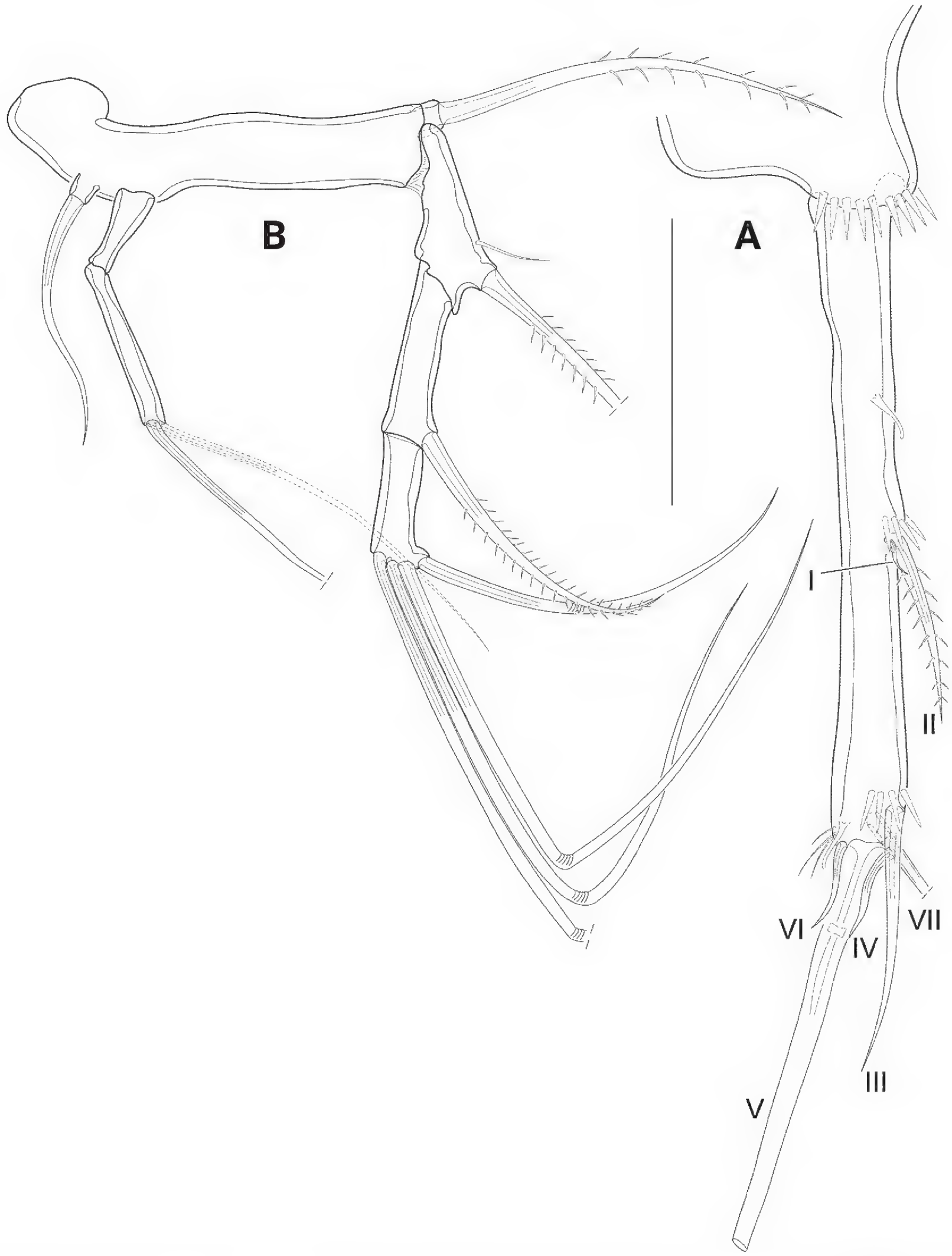

Figure 17. *Dorsiceratus andeep* sp. nov., holotype, female, east of Antarctic Peninsula, station #133/8-C. **A.** Left FR, ventral view; **B.** P1. Scale bar: 50 µm.

males by clear (but not sexually dimorphic) characters. The derived lack of inner setae on the third exopodal segments of P2–P4, which does not occur in any other *Dorsiceratus* species, is not interpreted here as a sexual dimorphic character, because no sexual dimorphism has been observed on those segments in *Dorsiceratus* to date. The armouring of the P5 basoendopod also distinguishes the female from the males; the latter bear 1 seta and 1 tube pore (Table 5; not documented for *Do.* 37), while the female is equipped with 2 setae but no tube pore. We conclude from this that at least two different *Dorsiceratus* species were detected at station #133.

Table 5. *Dorsiceratus andeep* sp. nov., setation of swimming legs P1–P4. Roman numerals indicate outer setae.

	Exopod	Endopod
P1	0-1; 0-1; 0-2-II	0; 0-2-0
P2	0-1; 1-1; 0-2-II+tube pore	0; 0-1-0
P3	0-1; 1-1; 0-2-II+tube pore	0; 0-2-0
P4	0-1; 1-1; 0-2-II	0; 0-2-0

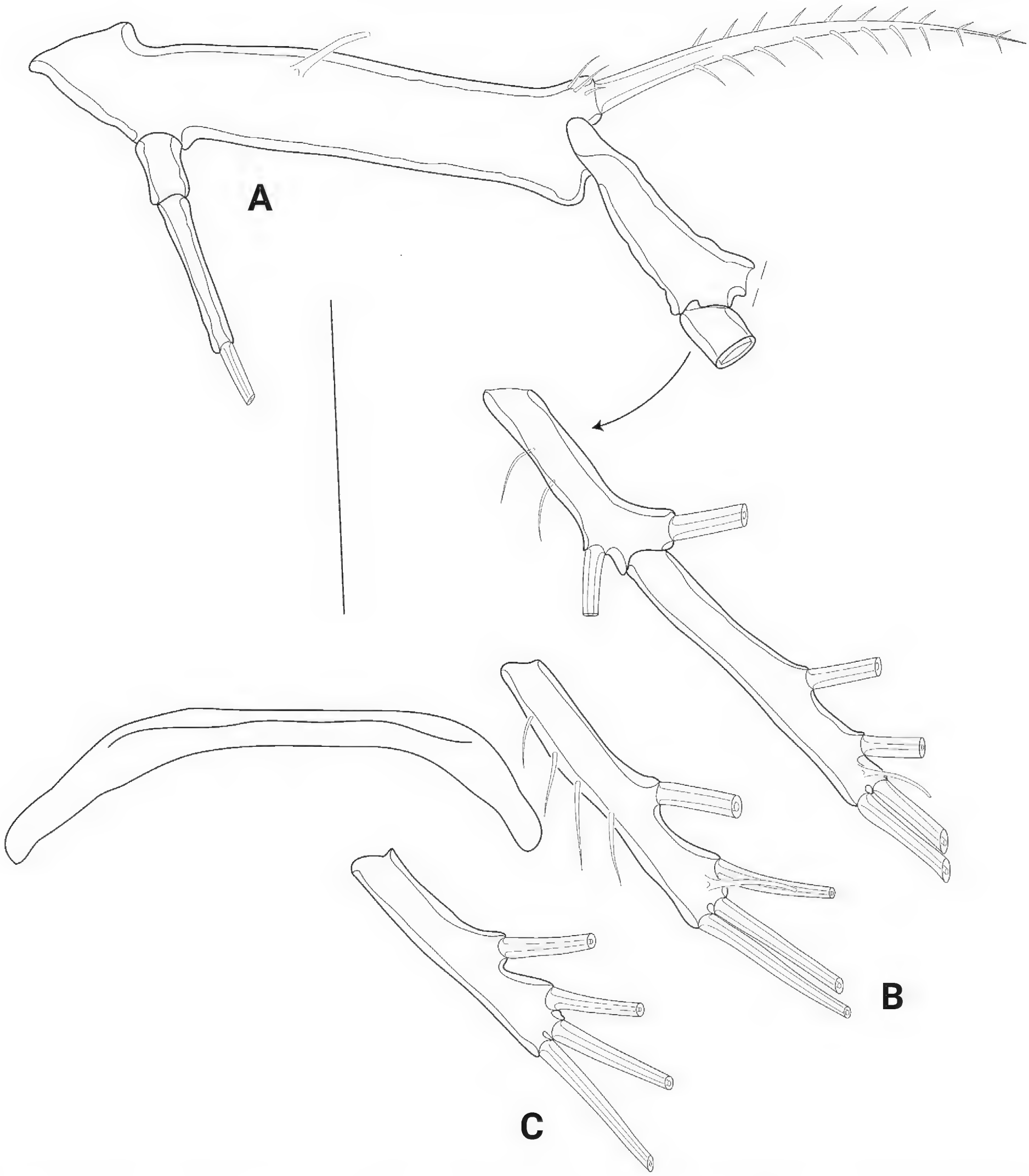

Figure 18. *Dorsiceratus andeep* sp. nov., holotype, female, east of Antarctic Peninsula, station #133/8-C. **A.** P2, with intercoxal sclerite and exp2 and exp3 drawn separately; **B.** P3 exp3; **C.** P4 exp4. Scale bar: 50 µm.

Tentative definition of the morphotypes 1–7 and a remaining "morpho-group"

Despite the high similarity in body shape (Fig. 19) and the structure of almost all extremities, which makes species recognition and the assignment of individuals extremely difficult, an attempt was made to group those individuals that could not be assigned to any of the known or newly described species into morphotypes on the basis of a comparison of selected characters (Table 6). This was done in a purely typological manner. In addition to a direct comparison of the individuals, the approach of a similarity analysis was chosen, which is rather unconventional for systematic studies. It included the known species and all 57 individuals and, in addition to pure presence-absence data, e.g., of setae or tube pores, also included morphometric values (body length, length-to-width ratio of the furcal rami), which were standardised for this purpose:

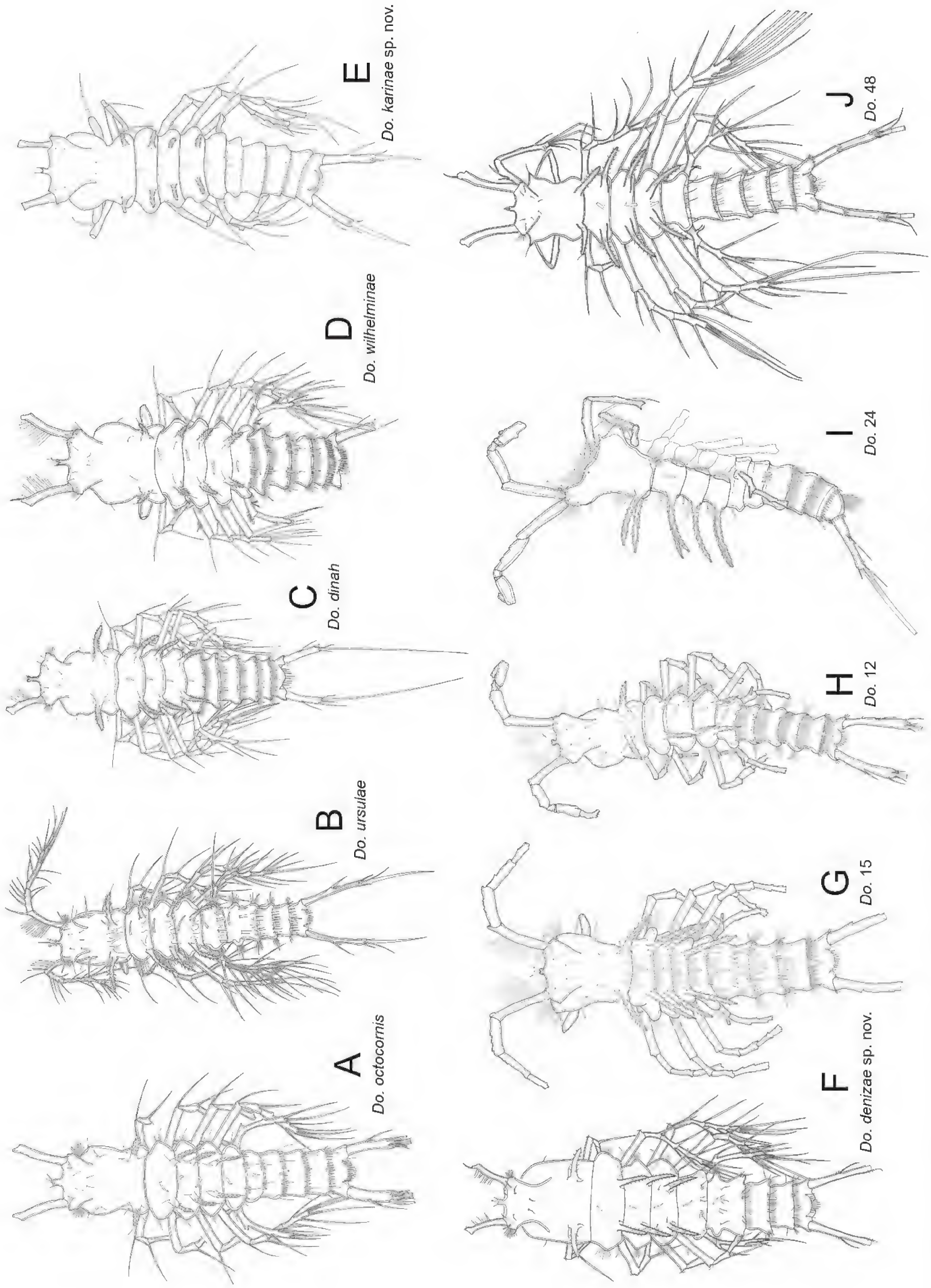

Figure 19. Habitus (dorsal/lateral view) of 10 different *Dorsiceratus* species/specimens to illustrate their high morphological similarity.

Table 6. Character matrix on which the similarity analysis was based. **BL ratio** = body length ratio; **FRL ratio** = furcal rami length ratio; **Md p/s1** = mandibular palp seta 1:1 = absent, 0 = present; **P1 e sg** = P1 exopod with 2 segments: 2, with 2 segments but suture still discernible: 1, with 3 segments: 0; **P1 b i/s** = P1 basis inner seta tiny: 1, inner seta long: 0; **P1 e-3 TP** = P1 exp3 with TP: 1, without TP: 0; **P2 e-3 TP** = P2 exp3 with TP: 1, without TP: 0; **P2–P4 e-3 is** = P2–P4 exp3 lacking inner seta(e): 1, seta(e) present: 0; **P3 e-3 TP** = P3 exp3 with TP: 1, without TP: 0; **P4 e-3 TP** = P4 exp3 with TP: 1, without TP: 0; **P5 e-b f** = P5 basoendopod and exopod fused: 1, distinct: 0; **P5 b s** = P5 basoendopod lacking setae: 2, with 1 seta: 1, with 2 setae: 0; **P5 b TP** = P5 basoendopod lacking tube pores: 2, with 1 tube pore: 1, with 2 tube pores: 0.

Species /specimen	BL ratio	FRL ratio	Md p/s1	P1 e sg	P1 b i/s	P1 e-3 TP	P2 e-3 TP	P2-P4 e-3 is	P3 e-3 TP	P4 e-3 TP	P5 e-b f	P5 b s	P5 b TP
Do. octocornis	0.48	0.36	0	2	0	0	1	0	1	1	1	1	0
Do. triarticulatus	0.69	0.67	1	0	1	0	1	0	0	0	0	0	0
Do. ursulae	0.46	0.50	0	1	0	0	1	0	1	1	0	0	0
Do. dinah	0.39	0.37	0	2	0	1	1	0	1	1	0	1	1
Do. wilhelminae	0.41	0.36	0	2	0	1	1	0	1	1	0	0	0
***Do.* 1**	0.65	0.50	0	0	0	0	1	0	0	0	0	0	0
***Do.* 2**	0.75	0.63	0	0	0	0	1	0	0	0	0	0	0
***Do.* 3**	0.74	0.66	0	0	0	0	1	0	0	0	0	1	0
***Do.* 4**	0.00	0.00	0	0	0	0	1	0	0	0	0	1	1
***Do.* 5**	0.61	0.54	0	0	0	0	1	0	0	0	0	0	0
***Do.* 6**	0.68	0.55	0	0	0	0	1	0	0	0	0	0	0
***Do.* 7**	0.62	0.55	0	0	0	0	1	0	0	0	0	0	0
***Do.* 8**	0.67	0.52	0	0	0	0	1	0	0	0	0	0	0
***Do.* 9**	0.69	0.57	0	0	0	0	1	0	0	0	0	0	0
***Do.* 10**	0.89	0.68	0	0	0	0	1	0	0	0	0	0	0
***Do.* 11**	0.61	0.49	0	0	0	0	1	0	1	0	0	0	0
***Do.* 12**	0.59	0.55	0	0	0	0	1	0	0	0	0	1	1
***Do.* 13**	0.55	0.52	0	0	0	0	1	0	0	0	0	1	1
***Do.* 14**	0.84	0.74	0	0	0	0	1	0	0	0	0	0	0
***Do.* 15**	0.61	0.55	0	0	0	0	1	0	1	0	0	0	0
***Do.* 16**	0.61	0.44	0	0	0	0	1	0	0	0	0	0	0
***Do.* 17**	0.71	0.82	0	0	0	0	1	0	0	0	0	1	0
***Do.* 18**	0.59	0.43	0	0	0	0	1	0	0	0	0	0	1
***Do.* 19**	0.63	0.58	0	0	0	0	1	0	0	0	0	0	0
***Do.* 20**	0.77	0.81	0	0	0	0	1	0	1	0	0	1	0
***Do.* 21**	0.53	0.49	0	0	0	0	1	0	0	0	0	1	1
***Do.* 22**	0.58	0.53	0	0	0	0	1	0	0	0	0	0	0
***Do.* 23**	0.63	0.54	0	0	0	0	1	0	0	0	0	0	1
***Do.* 24**	0.52	0.48	0	0	0	0	1	0	0	0	0	0	0
***Do.* 25**	0.53	0.47	0	0	0	0	1	0	0	0	0	1	1
***Do.* 26**	0.65	1.00	0	0	0	0	1	0	0	0	0	1	1
***Do.* 27**	0.74	0.56	0	0	0	0	1	0	0	0	0	0	0
***Do.* 28**	0.61	0.52	0	0	0	1	1	0	0	0	0	0	0
***Do.* 29**	0.51	0.42	0	0	0	0	1	0	0	0	0	1	1
***Do.* 30**	0.64	0.49	0	0	0	0	1	0	0	0	0	0	0
***Do.* 31**	0.00	0.48	0	0	0	0	1	0	0	0	0	0	0
***Do.* 32**	1.00	0.48	0	0	0	0	1	0	0	0	0	0	0
***Do.* 33**	0.56	0.43	0	0	0	0	1	0	0	0	0	1	1
***Do.* 34**	0.50	0.49	0	1	0	0	1	0	0	0	0	0	0
***Do.* 35**	0.53	0.45	0	0	0	0	1	0	0	0	0	0	0
***Do.* 36**	0.56	0.43	0	0	0	0	1	0	0	0	0	0	0
***Do.* 37**	0.58	0.69	0	0	0	0	1	0	0	0	0	0	0
***Do.* 38**	0.82	0.64	0	0	0	0	1	1	1	1	0	0	2
***Do.* 39**	0.57	0.53	0	0	0	0	1	0	0	0	0	1	1
***Do.* 40**	0.59	0.48	0	0	0	0	1	0	0	0	0	1	1
***Do.* 41**	0.72	0.69	0	0	0	0	1	0	0	0	1	0	2
***Do.* 42**	0.37	0.34	0	2	0	0	1	0	0	0	0	1	1
***Do.* 43**	0.47	0.34	0	2	0	0	1	0	0	1	0	1	1
***Do.* 44**	0.38	0.30	0	2	0	0	1	0	0	0	0	1	1
***Do.* 45**	0.43	0.30	0	2	0	0	1	0	0	0	0	1	1
***Do.* 46**	0.53	0.44	0	0	0	0	1	0	0	0	0	1	1
***Do.* 47**	0.49	0.43	0	0	0	0	1	0	0	0	0	0	0
***Do.* 48**	0.59	0.45	0	0	0	0	1	0	1	0	0	1	1
***Do.* 49**	0.50	0.36	0	2	0	0	1	0	1	0	0	0	1
***Do.* 50**	0.47	0.40	0	2	0	0	1	0	1	0	0	0	1
***Do.* 51**	0.38	0.32	0	2	0	0	1	0	1	0	0	0	1
***Do.* 52**	0.43	0.30	0	2	0	0	1	0	1	0	0	0	1
***Do.* 53**	0.56	0.38	0	2	0	0	1	0	1	0	0	0	1
***Do.* 54**	0.53	0.42	0	2	0	0	1	0	1	0	0	0	1
***Do.* 55**	0.41	0.35	0	2	0	0	1	0	1	0	0	0	1
***Do.* 56**	0.36	0.33	0	2	0	0	1	0	1	0	0	0	1
***Do.* 57**	0.60	0.43	0	0	0	0	1	0	0	0	0	0	0

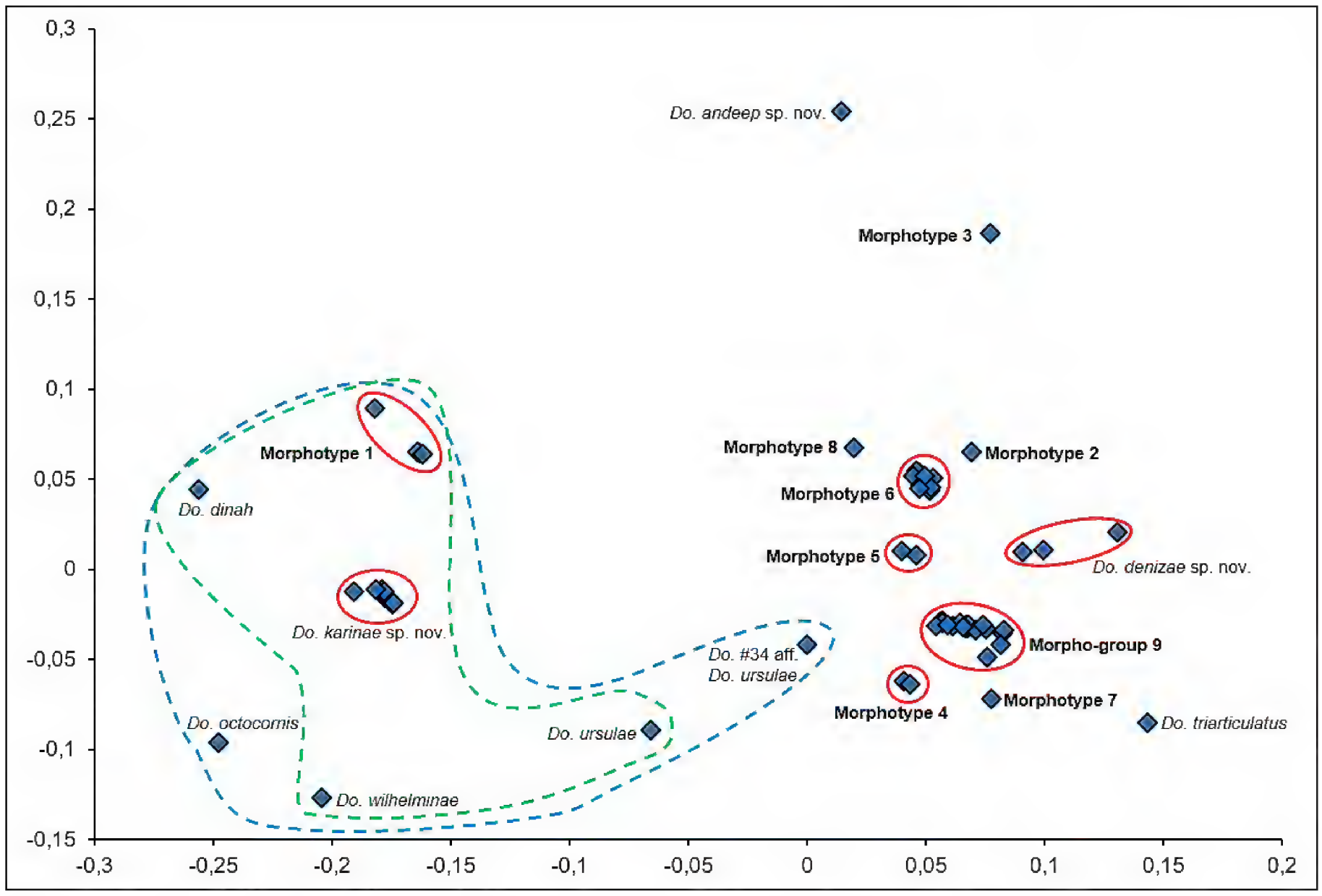

Figure 20. Ordination plot of a non-metrical Multidimensional Scaling (nMDS), based on a similarity analysis (Euclidean Distance, stress: 0.07903) of characters listed in Tab. 6. The single species/specimens are depicted as blue rhombi, and those species/morphotypes (and likewise "morpho-group" 9) enclosing > 1 individual are encircled in red. For the species assigned to the morphotypes, see Table 2. Blue dashed line borders all species/morphotypes that are characterised by a 2-segmented P1 exopod; green dashed line encircles those species/morphotypes that were reported from seamounts.

the greatest body/FR length ratio was equated with 1, whilst the remaining corresponding lengths were then set in relation to this. For the presentation of the results of the similarity analysis (coefficient: Euclidean distance), an ordination plot (nMDS) was chosen instead of a cluster analysis in order to avoid that the resulting dendrogram of the latter might be read as a systematic cladogram.

The result of the similarity analysis is shown in Fig. 20. Notwithstanding the typological approach, some interesting aspects can be observed. Thus, based on the available characters, all known and the newly described species can be well distinguished from each other and from the other individuals, apart from slight uncertainties in *Do. denizae* sp. nov. Specimen *Do.* 20 differs somewhat from the other two females, which is probably due to the presence of a tube pore on P3 exp3 in this female.

There is a remarkable correspondence between the structure of the P1 exopod and the location where the organism was found. Those species/individuals with a 2-segmented P1 exopod (Fig. 20, blue dashed line) were found on seamounts (Fig. 20, green dashed line), regardless of the geographical region (Atlantic, Mediterranean Sea). The only exception is male *Do.* 34, which was found in GB_{W1} but is morphologically similar to *Do. ursulae* from the GMS.

Dorsiceratus morphotype 1 (specimens *Do.* 42–*Do.* 45)

The four individuals, which are summarised as morphotype 1 (Table 2, Fig. 20), were all found on the Anaximenes seamount. They are further characterised by (i) a relatively small body size (362–457 µm, mean = 401 µm), (ii) furcal rami at most four times as long as wide, (iii) P1 exopod with only 2 segments, (iv) distinct P5 exopod, and (v) P5 basoendopod with only 1 seta and 1 tube pore each (not recognisable in *Do.* 42). It is noticeable that *Do.* 43 stands somewhat apart. This can be explained by the fact that this female has even shorter FR than the others (l/w ratio: 3 instead of 4) and that it is the only one with a tube pore on P3 exp3 (Table 2).

Dorsiceratus morphotype 2 (specimen *Do.* 26)

This group (Fig. 20) is represented by only one female specimen, *Do.* 26 (Table 2), which (i) originates from the northern Angola Basin (Table 1), (ii) is 1.5 times larger than the representatives of morphotype 1 (631 µm), and (iii) has very long FR (l/w ratio: 8). Further characters (e.g., the structure and armouring of the P1 exopod) cannot be considered due to the damage of the female.

Dorsiceratus morphotype 3 (specimen *Do.* 41)

The only representative of this group (i) was found in the Clarion-Clipperton Fracture Zone (Table 1), (ii) with almost 700 µm (Table 2), the female is even longer than morphotype 2 and (iii) also bears very long FR (l/w ratio: 7). In addition, (iv) the P5 basoendopod and exopod are fused as in *Do. octocornis*, and (v) the P5 basoendopod bears two setae but no tube pore.

Dorsiceratus morphotype 4 (specimens *Do.* 11, *Do.* 15)

Two females (i) from the same station in the Angola Basin (Table 1: *Do.* 11, *Do.* 15), which (ii) share the same body size (590 µm, 596 µm) and (iii) a similar FR length (Table 2: l/w ratio: 5, 6/). Moreover, (iv) both have 1 tube pore at P3 exp3. The other characters correspond to the condition assumed for the *Dorsiceratus* groundpattern.

Dorsiceratus morphotype 5 (specimens *Do.* 18, *Do.* 23)

Two females, (i) also from the Angola Basin (Table 1: *Do.* 18, *Do.* 23). They are similar in body size to morphotype 4 (Table 2), (ii) but have smaller FR length ratios (Table 2: l/w ratio: 4, 3), (iii) no tube pore on P3 exp3, but (iv) only 1 tube pore on P5 basoendopod.

Dorsiceratus morphotype 6 (specimens *Do.* 4, *Do.* 12, *Do.* 13, *Do.* 21, *Do.* 25, *Do.* 29, *Do.* 33, *Do.* 46)

A group of eight male individuals (Table 2). Morphotype 6 covers three geographical regions: the central Angola Basin (AB_C), the eastern Guinea Basin (GB_E), and the Brazil Basin (BB). Nevertheless, the nMDS (Fig. 20) shows that the individuals cluster closely based on the selected characters. However, the character states vary greatly (Table 2); the body size between 495 µm and 576 µm, and the FR-l/w ratio between 4 and 6. A common deviation refers to the ornamentation of the P5 basoendopod: it bears each 1 seta and 1 tube pore.

Dorsiceratus morphotype 7 (specimen *Do.* 28)

It is difficult to assign the only representative of this morphotype, a female from the eastern Guinea Basin (Tabs 1, 2: *Do.* 28), to one of the species or to another morphotype. The individual shows hardly any distinctive features. (i) Its body size (595 µm) is within the average of the species and individuals examined, (ii) it bears relatively short furcal setae (Table 2: l/w ratio: 4), and (iii) the P5 basoendopod bears the supposed plesiomorphic state of 2 setae and 2 tube pores. A special feature is the P1: (iv) The right exopod is 2-segmented but still shows the suture of the former boundary between exp2 and exp3, whereas the left exopod is clearly 3-segmented. However, this condition, which is also detectable in three other individuals (Table 2: *Do.* 10, *Do.* 12, *Do.* 46), is probably due to a malformation rather than a species-specific character and may therefore be irrelevant for a systematic classification. In addition (v), the last exopodal segment of the P1 bears a tube pore. This might be the main reason why *Do.* 28 is placed separately in Fig. 20.

Dorsiceratus morphotype 8 (specimen *Do.* 48)

Figs 21–25

On RV METEOR expedition M63/2 DIVA 2, a male was found in the western Guinea Basin (GB_{W2}) that appeared to belong to *Dorsiceratus denizae* sp. nov. on first comparison. However, despite its great similarity to the females, it also exhibits some differences that are not considered sexual dimorphisms but in favour of *Do.* 48 representing a different species. Thus, it is described here in full, and its classification is made just typologically as morphotype 8 until further records can provide definitive clarity. The male specimen was collected on 23.03.2005 at station #100/6, geographic position 0°37.2'N, 6°28.1'W, depth 5,167 m (Table 1).

Description of male. Habitus (Fig. 21A) long and slender (body length from rostral tip to end of furca 569 µm). Cephalothorax and P2–P4-bearing thoracic body somites, each with CLDP, respectively DT1–DT3, on posterior margins. Processes (Fig. 21B) cylindrical, covered with spinules, and carrying a sensillum at their tips. Cephalothoracic peak (Fig. 23A) well-developed; CLVEa well-developed. First two abdominal somites posteriorly with 2 sensilla each, a row of spinules, and a row of long hair-like spinules on ventral and dorsal margins. Rostrum (Fig. 23A) fused with cphth, small and constricted, nearly squared, slightly cleft at its tip, with terminal pair of sensilla and single tube pore medially. Telson broader than long; anal operculum with strong spinules and flanked by a pair of sensilla.

Note. Tube pores and sensilla on cphth and prosomal somites could not be observed in sufficient detail and are not drawn.

FR (Fig. 23B) long and slender, l/w ratio = 7, bearing 7 setae: seta I minute, accompanying II; seta II bipinnate, displaced on the ventral side and basally surrounded by row of spinules; seta III bipinnate, inserting subapically on ventral outer margin, accompanied by 4 spinules basally; seta IV (broken in Fig. 23B) minute, bare, apically on outer margin; seta V (broken in Fig. 23B) longest and bipinnate; seta VI bare, as long as seta IV, inserting apically on inner margin, basally accompanied by few spinules; seta VII bare and bi-articulated, located subapically at dorsal side; subapical tube pore not discernible.

A1 (Fig. 22A) 6 segmented, haplocer. First segment longest, with long spinules on inner margin and with 1 unipinnate seta on inner distal corner; second segment shorter than first, with 6 setae (4 bare, 1 broken, 1 bipinnate); third segment small, with 6 setae (3 broken); fourth

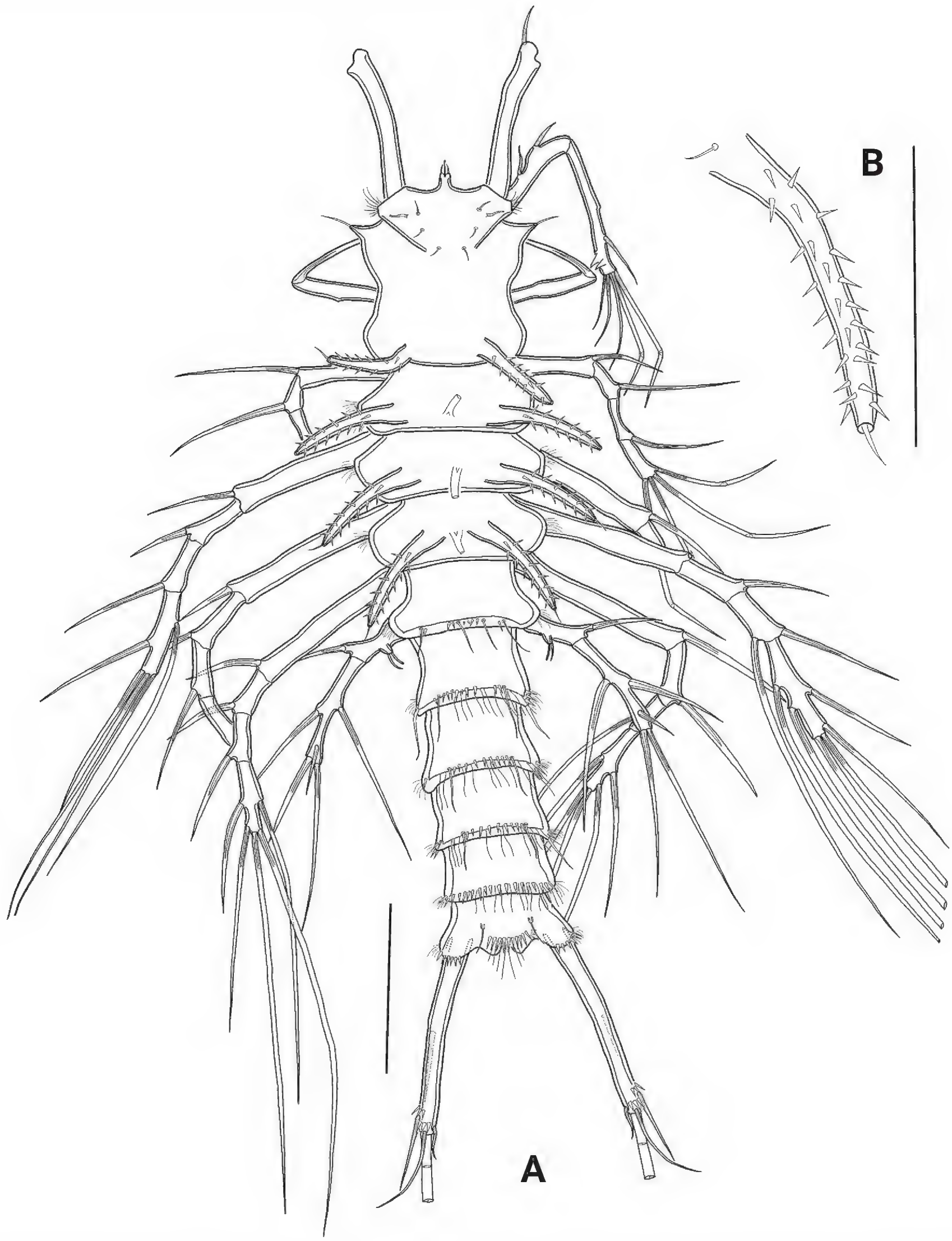

Figure 21. *Dorsiceratus* sp., morphotype 8 (*Do.* 48), male, western Guinea Basin, station #100/6. **A.** Habitus, dorsal view; **B.** Detailed view of right spinulose cuticular process DP3. Scale bars: 100 µm (**A**); 50 µm (**B**).

segment very small (arrowhead in Fig. 22A), unarmoured; fifth and sixth segments of almost same size, fifth segment with 11 setae: 9 small setae on anterior surface, 1 long bare seta arising together with aes from subapical acrothek, which is accompanied by 1 further long bare seta; sixth segment with 8 bare setae (4 of which bi-articulate, 2 of which tri-articulate) and 1 small aes. Armature Formula: I-1; II-6; III-6; IV-0; V-10 + (1 +aes); VI-7 + (1 + aes).

A2 (Fig. 23C) lacking exp. Allobasis with row of spinules and 2 unipinnate abexopodal setae. Endopod 1-segmented, laterally with several long spinules, 2 unipinnate spines, and 1 bare fine seta; terminally with 3 long geniculate setae, 1 small bare seta, and 2 unipinnate setae.

Md (Fig. 24A) coxa with several spinules. Gnathobase elongate, with several partly multicuspidate teeth. Basis, endo- and exopod fused to a long spinulose mandibular

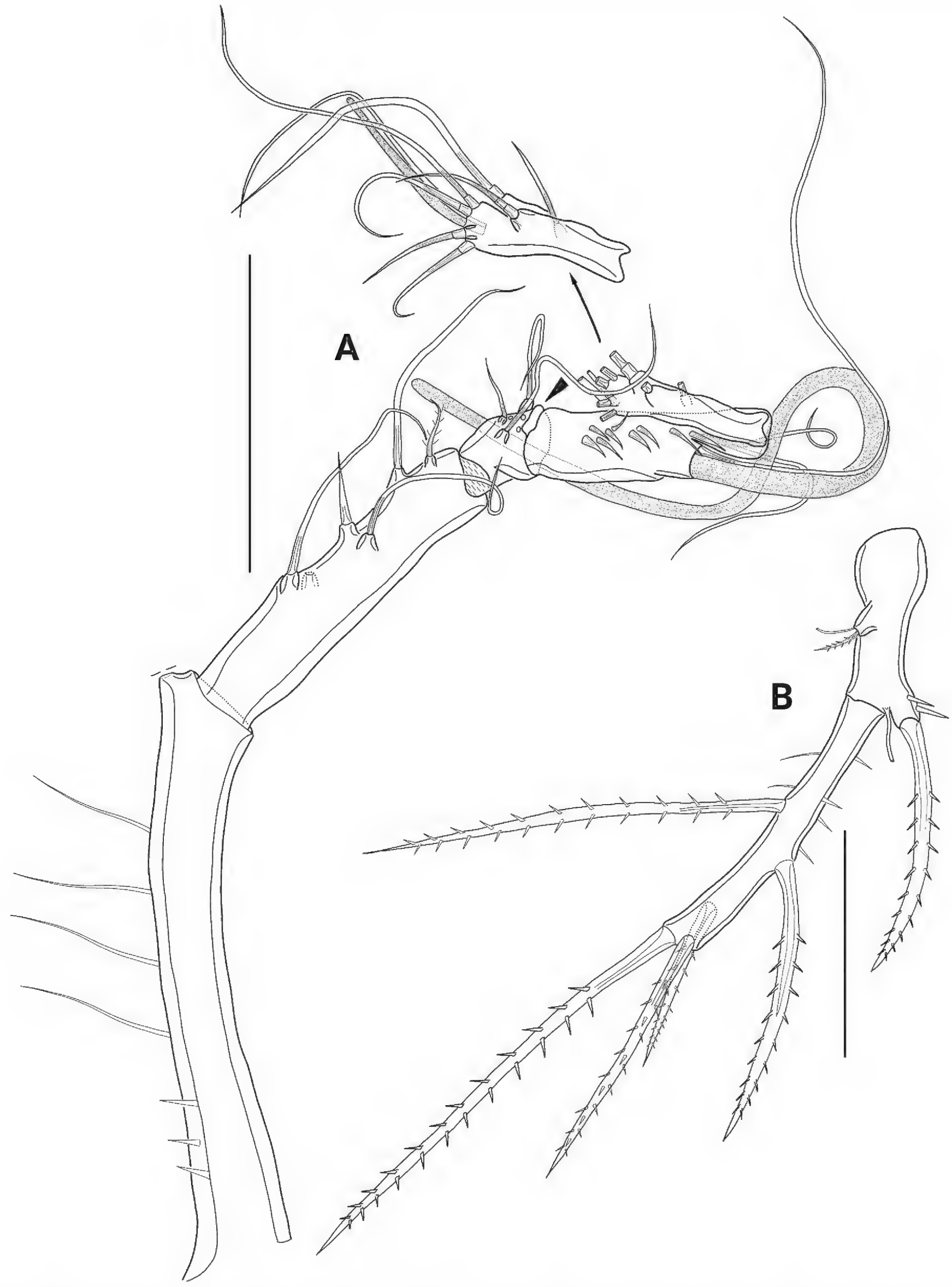

Figure 22. *Dorsiceratus* sp., morphotype 8 (*Do*. 48), male, western Guinea Basin, station #100/6. **A.** A1, the setation of the terminal segment shown separately; **B.** P5. Scale bar: 50 µm.

palp carrying 2 basal, 3 endopodal, and 1 exopodal seta (setae 1 and 2, 3–5, and 6, respectively; see figure).

Mxl (Fig. 24B) arthrite of praecoxa terminally with 6 strong spines, subapically with additional spine and 3 setae, one of which bifid, and with 2 surface setae and row of spinules. Coxal endite with 1 bare and 1 unipinnate seta. Basis, enp and exp fused, forming a single segment; basal endite with 3 apical setae and 1 subapical seta, exopod represented by 1 seta, endopod represented by 3 setae.

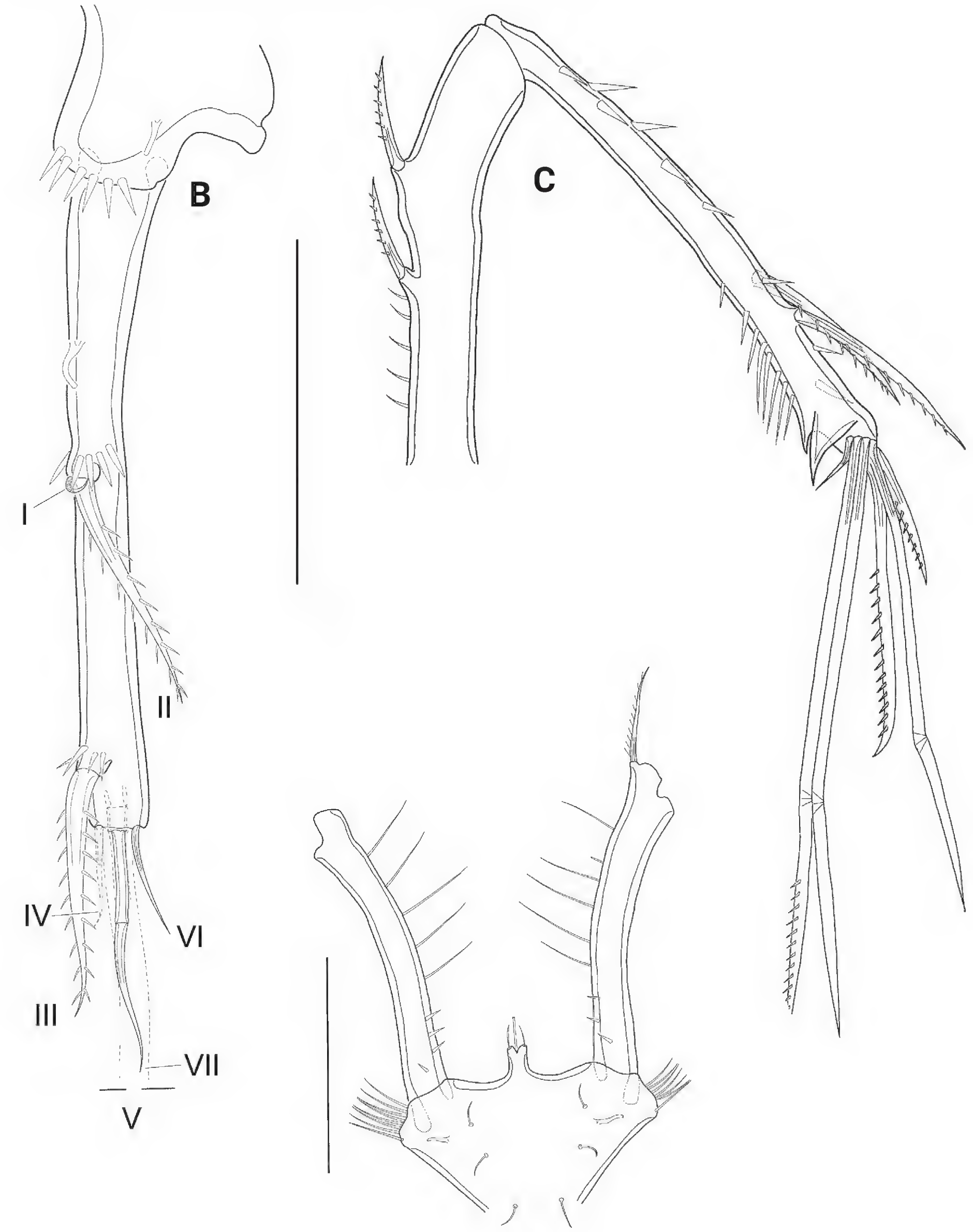

Figure 23. *Dorsiceratus* sp., morphotype 8 (*Do.* 48), male, western Guinea Basin, station #100/6. **A.** Frontal cephalothoracic peak with rostrum and first antennular segments; **B.** Right FR, ventral view, with numbered setae; **C.** A2. Scale bars: 50 μm.

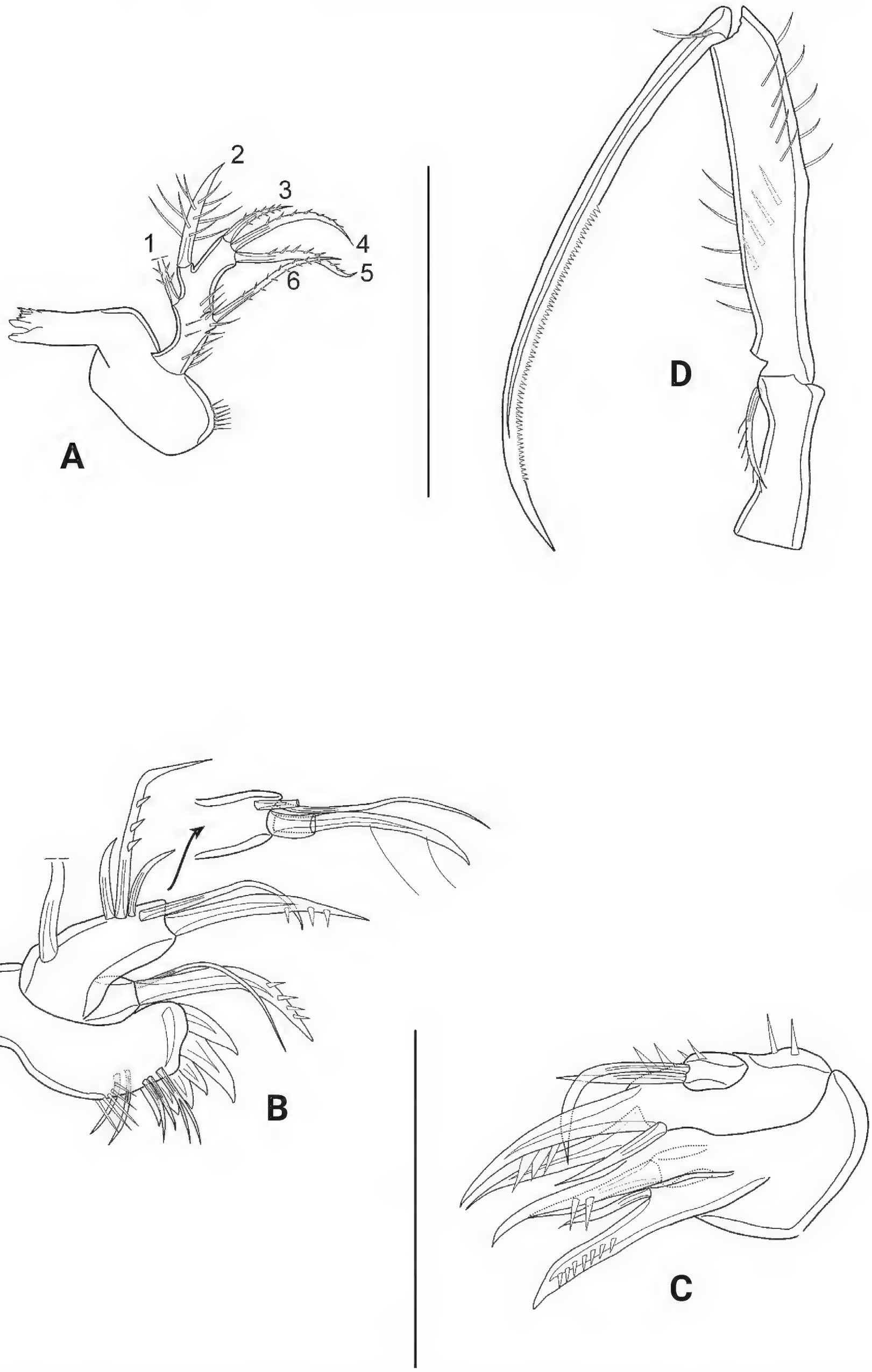

Figure 24. *Dorsiceratus* sp., morphotype 8 (*Do.* 48), male, western Guinea Basin, station #100/6. **A.** Md, with numbered setae of md palpus; "supernumerary" seta 1 broken; **B.** Mxl; **C.** Mx; **D.** Mxp. Scale bars: 50 µm.

Mx (Fig. 24C) syncoxa and allobasis separate, the former with 2 endites with 1 strong unipinnate seta fused to segment and 1 bare seta each. Allobasis with 1 unipinnate strong claw-like spine fused with segment, additionally with 1 strong and 1 bare seta. Endopod distinct, one-segmented, bearing 2 bare setae.

Mxp (Fig. 24D) prehensile, syncoxa half as long as basis, with uniplumose seta apically; basis with long spinules; enp produced into long, bare, but finely serrated claw, basally accompanied by small seta.

P1 as in *Do. denizae* sp. nov.

P2–P4 (Fig. 25A–D) with transversely strongly elongated bases easily observable in dorsal aspect of the habitus (cf. Fig. 21A), carrying a bipinnate outer seta, a long tube pore, and several spinules (exemplified for all three swimming legs in Fig. 25A). Exopods 3-segmented, exp1 and exp2 of nearly the same length, exp3 longest. All exopodal segments with slender outer spine(s). Exp1 without, exp2 with 1 inner seta. Exp3 with 2 apical setae and 2 outer spines; P2 and P4 exp3 with 1, P3 exp3 (Fig. 25C) with 2 inner setae; P2 exp3 with 1, P3 exp3 with 2 tube pores. P2 and P4 endopods (Fig. 25A, B) 2-segmented, enp1 small, lacking setae but carrying a long tube pore in P2; P2 enp2 apically with 1 long biplumose seta, P4 enp2 with 2 apical biplumose setae and 1 outer bipinnate spine displaced anteriorly; P3 endopod (Fig. 25D) 3-segmented, enp1 as in P4; enp2 as long as whole exopod, slender, apically turning into outwardly curved apophysis; enp3 as small as enp1, apically with 2 biplumose setae. Setal formula as in Table 7.

Table 7. *Dorsiceratus* sp., morphotype 8 (*Do.* 48), setation of swimming legs P1–P4. Roman numerals indicate outer setae.

	Exopod	Endopod
P1	0-1; 0-1;0-2-II	0;0-2-0
P2	0-1; 1-1; 0-2-II+tube pore	0; 0-1-0
P3	0-1; 1-1; 0-2-II+2 tube pores	0; 0-0, apophysis; 0-2-0
P4	0-1; 1-1; 0-2-II	0; 0-2-0

P5 (Fig. 22B) with basis and endopod fused, basal part with outer bipinnate seta arising from short setophore and accompanied by 2 spinules and 1 long tube pore. Endopodal lobe strongly reduced, forming small projection, with 1 tiny bipinnate seta and 1 tube pore. Exopod distinct, slender, and longer than basoendopod, carrying 2 outer bipinnate setae, the distalmost shifted towards posterior surface; subapically on the outer margin with 1 multipinnate seta, apically and on inner margin with 1 longer bipinnate seta.

Remarks. A special feature of the only individual of morphotype 8 concerns the mandible. It still shows all 6 setae (Fig. 24A), which, according to George (2021), represent the groundpattern of the *Ceratonotus* group. A presumed autapomorphy of *Dorsiceratus* is, however, the completely reduced mandibular basal seta 1. This could be confirmed in all individuals examined here, with the exception of the above-described male morphotype 8. Nevertheless, we consider this to be an individual atavistic expression in this particular male specimen. In other words, we assume that the formation of the mandibular seta 1 in the male of morphotype 8 represents an individual genetic "setback" to ancestral genotypes, in the sense of a morphologically expressed malformation. Malformations in single individuals of the Harpacticoida are not uncommon (e.g., George 1997, 2008; George et al. in prep.). They include the atrophy of segments and setae, the suppression of their formation, or, as in the present case, the (presumed atavistic) retention of mandibular seta 1 that was reduced in the course of the phylogeny of *Dorsiceratus*. In fact, of all 57 individuals and known species analysed here, this seta only occurs in just one individual, namely *Do.* 48; in all other individuals and described species, this seta has been lost. If *Do.* 48 was indeed the representative of an as-yet-unknown species, which could be characterised by the fact that mandibular seta 1 was still present in all its representatives, then this circumstance would invalidate the presumed autapomorphic loss of that seta in *Dorsiceratus*. However, precisely because *Do.* 48 is actually the only specimen retaining that seta, we consider the assumption of an individual atavism to be more plausible than the assumption that the seta was still formed in the groundpattern of *Dorsiceratus*. In order to clarify this, further findings of specimens of *Dorsiceratus* are essential.

Dorsiceratus "morpho-group" 9 (specimens *Do.* 1, *Do.* 2, *Do.* 2, *Do.* 5–*Do.* 10, *Do.* 14, *Do.* 16, *Do.* 19, *Do.* 22, *Do.* 24, *Do.* 27, *Do.* 30–*Do.* 32, *Do.* 35–*Do.* 37, *Do.* 39, *Do.* 40, *Do.* 47, *Do.* 50):

Twenty-four of the individuals analysed form a clearly delimited cluster (Fig. 20) based on the characters selected for the similarity analysis (Table 6). It includes (i) representatives from almost all study areas (Table 1: GMS, EAP, AB_C, GB_{W1}, GB_E, east of Madeira) and is also characterised by a remarkable morphological heterogeneity, which is why we do not want to call it a reasonably uniform "morphotype". Thus (ii) the body lengths of the females alone vary between 563 µm and 971 µm, and (iii) the l/w ratio of the FR ranges between 4 and 9. The other comparative characters, however, are almost identical in the individuals. Morpho-group 9 thus summarises all specimens that cannot be assigned to a known species or to one of the morphotypes described here. Their representatives cannot currently be characterised by any aut- or synapomorphies. Morpho-group 9 thus confirms the assumption that molecular data are required for a clear characterisation of *Dorsiceratus* species. Future studies on this genus must take this into account.

The comparatively high similarity of two Antarctic male specimens of morpho-group 9 (Table 2: *Do.* 39,

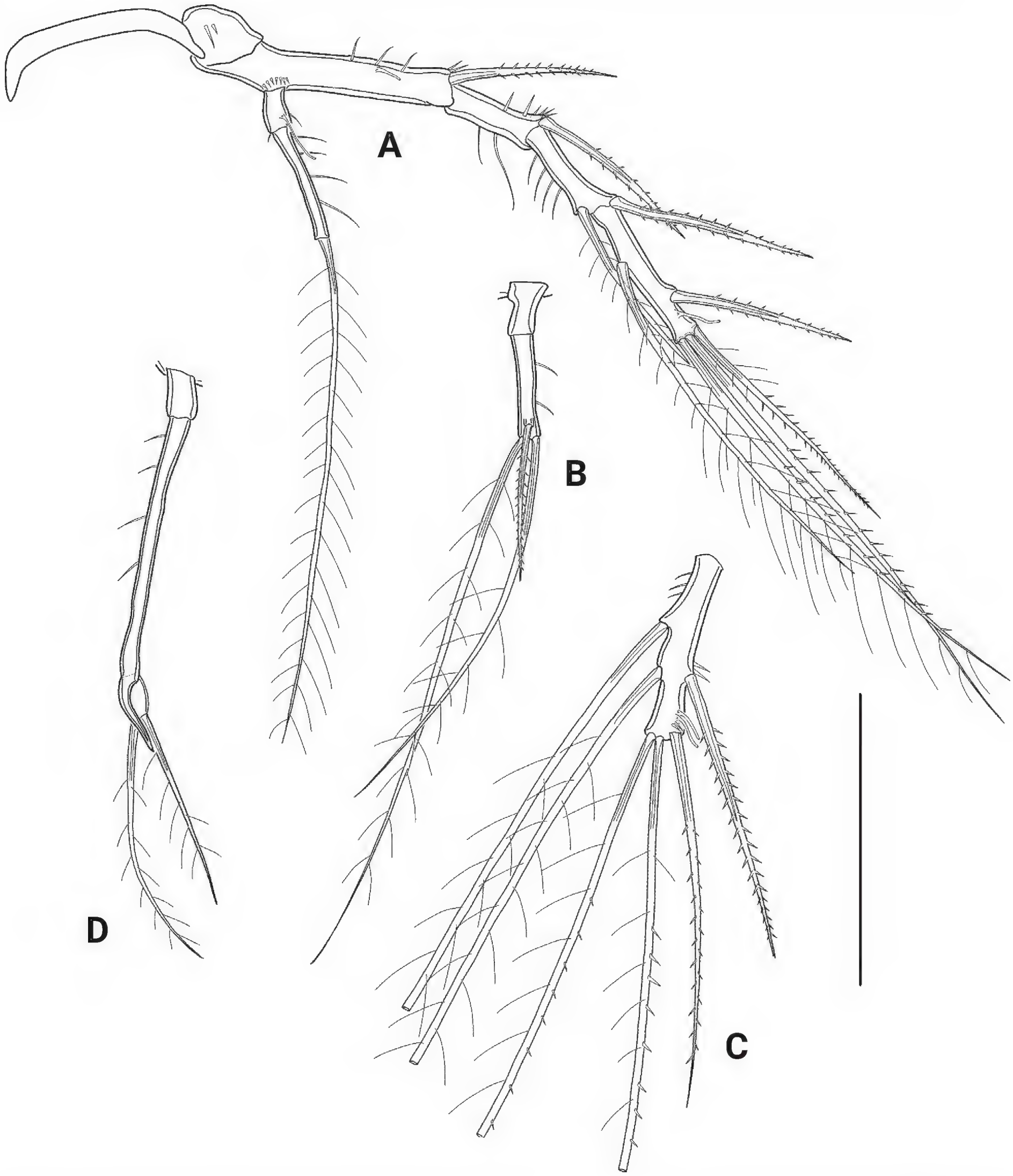

Figure 25. *Dorsiceratus* sp., morphotype 8 (*Do.* 48), male, western Guinea Basin, station #100/6. **A.** P2; **B.** P4 endopod; **C.** P3 exp3 showing the 2 tube pores; **D.** P3 endopod. Scale bar: 50 µm.

Do. 40) with the male labelled as morphotype 8 (tropical east Atlantic) is remarkable. As can be seen in Table 2, all three individuals have the same body dimensions and furcal l/w ratios. Moreover, the P5 basoendopod in all three specimens bears only 1 seta and 1 tube pore. Furthermore, they are neither assigned to morphotype 6, whose representatives also bear 1 seta and 1 tube pore each on the P5 basoendopod. However, a closer look reveals that the individuals of morphotype 6 tend to be smaller than those of morphotype 8 and *Do.* 39 and *Do.* 40, and the FR are also shorter (Table 2). The fact that morphotype 8 was not assigned to morpho-group 9 may be due to the P3 exp3, which has 2 tube pores.

Diagnostic identification key to the described *Dorsiceratus* species

1 P1 exopod 3-segmented 2
– P1 exopod 2-segmented 4
2 P2–P4 exp3 with 1:2:1 inner setae, respectively 3
– P2–P4 exp3 without inner setae ..... *Do. andeep* sp. nov.
3 Md palpus with 2 apical setae, P1 inner basal seta minute; female P5 basoendopod lacking setae and tube pores ..... *Do. triarticulatus* Coull, 1973
– Md palpus with 3 apical setae, P1 inner basal seta long; female P5 basoendopod with 1 seta and 2 tube pores ..... *Do. denizae* sp. nov.
4 P1 exopodal spine II displaced subapically 5
– P1 exopodal spine II still in medial position ..... *Do. ursulae* George, 2006
5 P1 exp2 subapically with tube pore; rostrum twice as long as broad 6
– P1 exp2 lacking tube pore; rostrum at most 1.5 times longer than broad 7
6 P1 exopodal element II a geniculate seta ..... *Do. dinah* George & Plum, 2009
– P1 exopodal element II a unipinnate spine ..... *Do. wilhelminae* George & Plum, 2009
7 Female P5 basoendopod fused with exopod, basoendopod with 1 seta and 2 tube pores ..... *Do. octocornis* Drzycimski, 1967
– Female P5 basoendopod and exopod distinct, basoendopod with 2 setae and 1 tube pore ..... *Do. karinae* sp. nov.

Discussion

Characterisation of a monophylum *Dorsiceratus* Drzycimski, 1967

George (2006a) postulated two autapomorphies to establish a monophylum *Dorsiceratus* [plesiomorphic condition in square brackets]:

1. P2 enp2 with 1 seta [with 2 setae];
2. P4 sexually dimorphic (female endopod lost the outer spine) [no sexual dimorphism (outer spine still present)].

Both George (2006a) and George and Plum (2009) considered these two evolutionary novelties to be weak because other representatives of the *Ceratonotus* group also show only 1 apical seta on P2 enp2 (character 1: *Tauroceratus tauroides* (George, 2006), *T. vareschii* (George, 2006), and possibly *Polyascophorus gorbunovi* (Smirnov, 1946) (cf. Smirnov 1946; George 2006b). Also, sexual dimorphism on P4 enp2 (character 2), in which the female loses the outer spine but the male retains it, can also be observed in certain other species (*Polyascophorus martinezi* George, 1998, *Pseudopolyascophorus monoceratus* (George, Wandeness & Santos, 2013), *Tauroceratus tauroides*) (cf. George 1998a, 2006b; George et al. 2013). Although males of several species of the *Ceratonotus* group are still unknown, which brings a certain hesitation in the evaluation of this character, it can be assumed with a fair degree of certainty that this sexual dimorphism was first developed within the *Ceratonotus* group. This can be seen in *Paratouphapleura aaroni* George, 2021, which retains the outer spine on both the male and the female (George 2021). Otherwise, the loss of this element in both sexes is also detectable in the *Ceratonotus* group: in *Arthuricornua anendopodia* Conroy-Dalton, 2001, *Dendropsyllus kimi* Lee & Huys, 2019, *De. magellanicus* (George, 1998), and *Dimorphipodia changi* Lee & Huys, 2019, both sexes have lost the outer spine (cf. George 1998a; Conroy-Dalton 2001; Lee and Huys 2019).

And yet, in our opinion, characters 1 and 2 retain their status as clear autapomorphies, on the basis of which *Dorsiceratus* can be well justified as a monophylum. The reduction of setae is common in Harpacticoida and often occurs convergently. This is probably also the case in the species of different genera mentioned above, whereas characters 1 and 2 already occur in the groundpattern of *Dorsiceratus*, as all known species and all other individuals examined here share both characters.

Careful comparative morphological analysis revealed another two characters that can be claimed to be autapomorphies of *Dorsiceratus*:

3. Loss of seta 1 of the md palpus [seta 1 still retained];
4. P2 exp3 with tube pore [lacking tube pore].

As noted above, all individuals examined here, as well as the known and newly described species, have lost the first exopodal seta on the mandibular palpus (character 3). The only exception is the male specimen, which was defined here as morphotype 8 (see discussion there). However, this apomorphy also occurs in some other representatives of the *Ceratonotus* group (*Dimorphipodia changi*, *Echinopsyllus*, *Pseudechinopsyllus sindemarkae* George, 2006) (cf. Conroy-Dalton 2003a; George 2006a; Wandeness et al. 2009). The extent to which character 3 may represent a synapomorphy of the taxa mentioned must be clarified in future studies. Nonetheless, because the remaining taxa of the *Ceratonotus* group show the plesiomorphic state (seta 1 still present), their reduction is not part of the groundpattern of the *Ceratonotus* group. In our opinion, there is evidence that this character evolved convergently in various of its representatives. Clear autapomorphies

prove that *Dimorphipodia changi* and *Ps. sindemarkae* can be unequivocally characterised as independent species and *Echinopsyllus* as a monophylum (George 2006a; Wandeness et al. 2009; Lee and Huys 2019). *Dorsiceratus* does not share the respective autapomorphies.

A possible but currently uncertain autapomorphy concerns the formation of a tube pore at P2 exp3 in *Dorsiceratus* (character 4). A tube pore also occurs sporadically on this segment in other species of the *Ceratonotus* group (*A. anendopodia*, *Ceratonotus elongatus* Gómez & Díaz, 2017, *C. pectinatus* Sars, 1909, *Dendropsyllus kimi* Lee & Huys, 2019, *De. thomasi* Conroy-Dalton 2003, *Di. changi*, *Polyascophorus martinezi*, *Poropsyllus menzelae* George, 2021, *Pseudopolyascophorus monoceratus*, *Touphapleura schminkei*) (cf. Sars 1909; George 1998a, 2021; Conroy-Dalton 2003b; George et al. 2013; Gómez and Díaz 2017; Lee and Huys 2019). The fact that *T. schminkei*, probably the most ancestral representative of the *Ceratonotus* group, already bears a tube pore could be an indication that its formation is already inherent in the groundpattern of the *Ceratonotus* group and that its absence in other species of the group is due to a later reduction. On the other hand, the formation of a tube pore in *T. schminkei* could also be a convergent new formation. Until clarification is achieved, we favour the latter assumption and postulate the formation of a tube pore at P2 exp3 as an autapomorphy of *Dorsiceratus*, which also occurred convergently in other species of the *Ceratonotus* group. Further below, we examine in detail the formation of tube pores in the *Ceratonotus* group and their possible phylogenetic significance.

Characterisation of the known *Dorsiceratus* species: Current situation

Drzycimski's (1967) *Dorsiceratus octocornis* and Coull's (1973) *Do. triarticulatus* could be clearly distinguished from each other despite the basically great morphological similarity (Coull 1973: 619: "...A1, A2, and the mouthparts are almost identical in the two species..."):

A. P1 exopod 2-segmented in *Do. octocornis*, 3-segmented in *Do. triarticulatus*;
B. P5 exopod of the female fused with the basoendopod in *Do. octocornis* but separated in *Do. triarticulatus*;
C. Furcal rami are comparatively short in *Do. octocornis* (l/w ratio: 4) and much longer in *Do. triarticulatus* (l/w ratio: 7).

Even George's (2006a) *Do. ursulae* could still be quite clearly distinguished from the other two species, despite a great similarity (George 2006a: 142):

D. Although the P1 exopod is 2-segmented as in *Do. octocornis*, its basic structure in *Do. ursulae* is still like that of a 3-segmented exopod; the former separation of exp2 and exp3 is still recognisable by a superficial suture, and the proximal outer spine (element II, cf. George 2020) of the former exp2 is still in its original position and is not displaced subapically as in *Do. octocornis*.
E. The length of the FR (l/w ratio: 6) lies between the other two species in *Do. ursulae*.

This may give the impression that *Do. ursulae* (location: GMS in the middle of the Atlantic) occupies an intermediate position between *Do. triarticulatus* found in the north-west Atlantic and *Do. octocornis* found in the north-east Atlantic.

In contrast, George and Plum (2009) had more difficulties establishing the two species, *Do. dinah* (SeiS) and *Do. wilhelminae* (SedS), which were also found in the middle of the Atlantic. Apart from the fact that both species could only be described on the basis of one badly damaged female each, George and Plum (2009) found that not all of the now five known *Dorsiceratus* species could be characterised by clear morphological differences, as is usually the case with Harpacticoida. They attempted to differentiate the five species phylogenetically (cf. George and Plum 2009, Table 4) and found potential autapomorphies for three species [plesiomorphic states in square brackets]:

Dorsiceratus dinah

5. Third abdominal somite with 2 tube pores dorsally [with 1 tube pore];
6. P1 exopodal seta II geniculated [seta not geniculated].

Dorsiceratus triarticulatus

7. P1 basis inner seta extremely reduced in size [seta long];
8. P1 enp2 with 1 apical seta [with 2 apical setae].

Dorsiceratus ursulae

9. Cphth and thoracic somites with several rows of fine "hairy" setules [lacking such setules];
10. FR is at least 5.5 times longer than broad [FR is at most 4 times longer than broad];
11. A1 female second segment with at most 6 setae [with at least 7 setae];
12. A1 female second segment with long spinules [lacking spinules];
13. A1 female fourth segment with at most 9 setae [with at least 10 setae].

George and Plum (2009, table 4) were unable to find potential autapomorphies for either *Do. octocornis* or *Do. wilhelminae*. Derived characters in one of the two species are also found in, at least, another species (e.g. the female P5 exopod fused with the basoendopod and armouring of the basoendopod with only 1 seta: *Do. octocornis* and *Do.*

dinah; row of long spinules on the A2 endopod in *Do. wilhelminae* and *Do. ursulae*; fusion of the endopod of the maxilla with the basis in *Do. wilhelminae* and *Do. triarticulatus*; a clearly elongated rostrum in *Do. dinah* and *Do. wilhelminae*; development of a 2-segmented P1 exopod, which all other species except *Do. triarticulatus* have; apical shortening of the former P1 exp3, which leads to the seta II now being located subapically instead of medio-laterally (*Do. octocornis*, *Do. dinah*, *Do. wilhelminae*).

This brief outline illustrates the difficult situation we faced when we tried to assign new *Dorsiceratus* specimens to known species or to describe them as scientifically new species. Even though it was stated at the beginning that representatives of this genus are found only rarely and in small numbers, the DZMB now holds 57 individuals from a wide variety of localities, which we hoped would enable us to characterise the taxon *Dorsiceratus* and the species assigned to it clearly and phylogenetically. However, the results of our comprehensive comparison are sobering. Even if derived characters are found in the different *Dorsiceratus* individuals, they do not help to characterise species clearly and phylogenetically. This is even more difficult because, as already mentioned at the beginning, a wealth of characters, such as the habitus, the structure, and the armouring of most extremities (A1, A2, mouthparts, P2–P4), are identical or almost identical in all five species. Despite the large number of individuals that were available for the study presented here, it was not possible to clearly distinguish species even from distant localities or to unambiguously group individuals from nearby or even the same localities into one species. Only the three species described here, *Do. andeep* sp. nov., *Do. denizae* sp. nov., and *Do. karinae* sp. nov., can be well justified (also phylogenetically).

In the following, we nevertheless attempt to provide arguments that support our assumptions. They are discussed in detail in separate sections.

Character selection

As already mentioned (Coull 1973; George 2006a; George and Plum 2009), representatives of *Dorsiceratus* are characterised by a conservative expression of morphological characters. Consequently, after careful examination, a number of characters had to be excluded from the comparison as irrelevant (expression and position of cuticular processes; structure and armour of the P2, the female P3 endopod, and the (male and female) P4 endopod). Other characters had to be disregarded because they have not been described in sufficient detail in the literature and could not be compared in several individuals of the material available to us due to damage (mouthparts, male P3 endopod, etc.). These circumstances forced us to resort to characters such as the occurrence and number of tube pores or morphometrically recorded data (length of habitus and furcal rami). Both are not easy to grasp and discuss phylogenetically. For example, is the formation of a tube pore on P3 exp3 a new formation in those individuals that possess it? An outgroup comparison shows that other members of the *Ceratonotus* group also have such a tube pore, which led George (2021) to assume that the formation of a tube pore was part of the groundpattern of the *Ceratonotus* group and that its absence, for example, in *Poropsyllus* George, 2021, and *Paratouphapleura* George, 2021 (both genera monotypic), should be interpreted as derived. We address this issue further below.

Table 6 lists the characters that we were able to use for our morphological comparison. They serve to differentiate morphotypes from each other in addition to the newly described species. However, we start with the phylogenetic characterisation of the genus and the species described so far.

Phylogenetic characterisation of the *Dorsiceratus* species described so far:

Remarks: A phylogenetic investigation of the closer relationships of the species characterised below is not carried out at this time. Although common characters, such as a 2-segmented P1 exopod or the formation and number of geniculate setae or of tube pores, may provide hints of possible close relationships (cf. Conroy-Dalton 2001; George 2006a; George and Plum 2009), their heterogeneous occurrence in the individuals examined here does not allow comparisons that go beyond a typologically orientated formation of hypothetical morphotypes.

Dorsiceratus andeep sp. nov.

Dorsiceratus andeep sp. nov. is also strikingly similar to all other representatives of *Dorsiceratus* in terms of its general appearance and the structure of its limbs but is nevertheless characterised by some exclusive morphological features. With a body length of 799 µm, it is the largest of all species described so far and the third largest of the individuals analysed here (Table 5, *Do.* 14: 820 µm, *Do.* 32: 971 µm). The l/w ratio of the FR with 8 is also particularly high; it only reaches an equally large or even higher value in two other individuals (Table 2, *Do.* 26: 8/1, *Do.* 37: 9/1). In addition, however, *Do. andeep* sp. nov. exhibits three characters (Fig. 18A–C) that undoubtedly represent an evolutionary novelty within *Dorsiceratus*, which is also relevant from a phylogenetic point of view [plesiomorphic expression in square brackets]:

14. P2 exp3 lacking inner seta [with 1 inner seta];
15. P3 exp3 lacking inner seta [with 2 inner setae];
16. P4 exp3 lacking inner seta [with 1 inner seta].

These three characters are unique within *Dorsiceratus*, especially as all species described and all individuals examined here even bear 2 inner setae on P3 exp3. Characters 14–16 are therefore postulated here as autapomorphies of *Do. andeep* sp. nov. They undoubtedly justify the establishment of this new species.

Dorsiceratus denizae sp. nov.

Apart from the comparatively large body size, which we are unable to determine phylogenetically, *Do. denizae* sp. nov. is characterised by the following autapomorphies:

17. FR seta II displaced ventrally [seta II inserting laterally];
18. FR seta III displaced ventrally [seta III inserting laterally];
19. (= character 11) A1 second segment with 6 setae [with at least 7 setae];
20. Female P5 basoendopod with 1 seta [with 2 setae].

Dorsiceratus denizae sp. nov. resembles *Do. triarticulatus* in some characters. It is slightly larger than the latter, has the same l/w ratio = 7 (Table 2), and has 3-segmented exopods on P1. However, characters 17, 18, 19 (11), and 20 characterise it as an independent species. The ventral displacement of the FR seta II (character 17) has so far only been observed in *Do. denizae* sp. nov. Also, the displacement of the FR seta III (character 18) is also hypothesised as an autapomorphy. Although this character also occurs in *Do. karinae* sp. nov. and in *Do. octocornis*, these two species bear a 2-segmented instead of a 3-segmented P1 exopod and have a number of other characters not shared by *Do. denizae* sp. nov. (see the corresponding characterisations). Thus, a convergent ventral displacement of seta III in the species mentioned is more plausible than the assumption that the displacement is an indication of a close relationship.

The loss of 1 seta on the second antennular segment (character 19) is a deviation shared with *Do. ursulae* (character 11; see characters listed above for *Do. ursulae*). Nonetheless, the same applies here as for character 18: The differences between the two species are so significant that a convergent reduction of the seta is assumed, and character 19 is interpreted as autapomorphic for *Do. denizae* sp. nov.

The loss of 1 seta on the female P5 basoendopod (character 20) while retaining 2 tube pores is again shared by *Do. denizae* sp. nov. with *Do. octocornis*, which also indicates convergence for the reasons mentioned above. Character 20 is therefore assumed to be autapomorphic for *Do. denizae* sp. nov.

Dorsiceratus dinah George & Plum, 2009

The above-mentioned autapomorphies 5 and 6 recognised by George and Plum (2009) withstood the comparison of this study and remain valid.

Dorsiceratus karinae sp. nov.

Dorsiceratus karinae sp. nov. can be characterised as a distinct species by two derived characters:

21. Furcal seta I completely lost [seta I present].
22. Proximal section of P1 exp3 strongly elongated [section of moderate length].

Within the *Ceratonotus* group, a gradual reduction in the size of the furcal seta I (character 21) can be observed (cf. George 2021). This reduction in size can go so far that the seta is not bigger than the surrounding fine spinules. In the past, this has led to seta I being overlooked in descriptions and consequently described as missing (cf. George and Schminke 1998; George 2006b). In the present case, special attention was therefore paid to seta I. In the eight individuals of the type material of *Do. karinae* sp. nov., neither the tiny seta itself nor its possible point of attachment was detectable. Therefore, furcal seta I is assumed by us to be completely reduced and thus missing. This condition is a unique derivation within the *Ceratonotus* group, and character 21 is therefore a strong autapomorphy for *Do. karinae* sp. nov.

In *Dorsiceratus* species with a 2-segmented P1 exopod, this gradually undergoes further transformations. For example, the exopodal section behind the outer spine II (Fig. 26, see also George 2020), which originally sat at the outer edge of the former exp2 (Fig. 26A–E), shortens so much that spine II appears to become more and more apically displaced (Fig. 26F) and finally inserts subapically (Fig. 26G–I; *Do. octocornis*, *Do. wilhelminae*, *Do. dinah*). Moreover, in *Do. karinae* sp. nov. the section in front of element II has undergone a particularly strong elongation (Fig. 26F). While in *Do. dinah*, *Do. octocornis*, *Do. ursulae*, and *Do. wilhelminae*, it presents l/w ratios of between 2.5 and 3.9; in *Do. karinae* sp. nov., it reaches a l/w ratio of 6.6. This pronounced elongation is interpreted here as an autapomorphy for that species.

Dorsiceratus octocornis Drzycimski, 1967 (type species)

As described above, no autapomorphies have been found to characterise *Do. octocornis* since the omission of the characters "P1 exopod 2-segmented" and "P1 exopodal seta II arising subapically" (George and Plum 2009). However, our comparison revealed five characters (cf. George 2006a, fig. 8A) that are missing not only in the other *Dorsiceratus* species and the other individuals studied here, but also within the entire *Ceratonotus* group. For the sake of simplicity, they are summarised as a character complex:

23–27: P5- and P6-bearing thoracic somites and the first 3 abdominal somites equipped with strong spinules dorsally on the posterior margin [corresponding body somites bearing at most small and fine spinules].

All other representatives of the *Ceratonotus* group, including the remaining *Dorsiceratus* species and the individuals examined here, have either no spinules at all or, at most, small, fine spinules on the indicated margins. Thus, *Do. octocornis* can be phylogenetically justified as an independent species without any doubt.

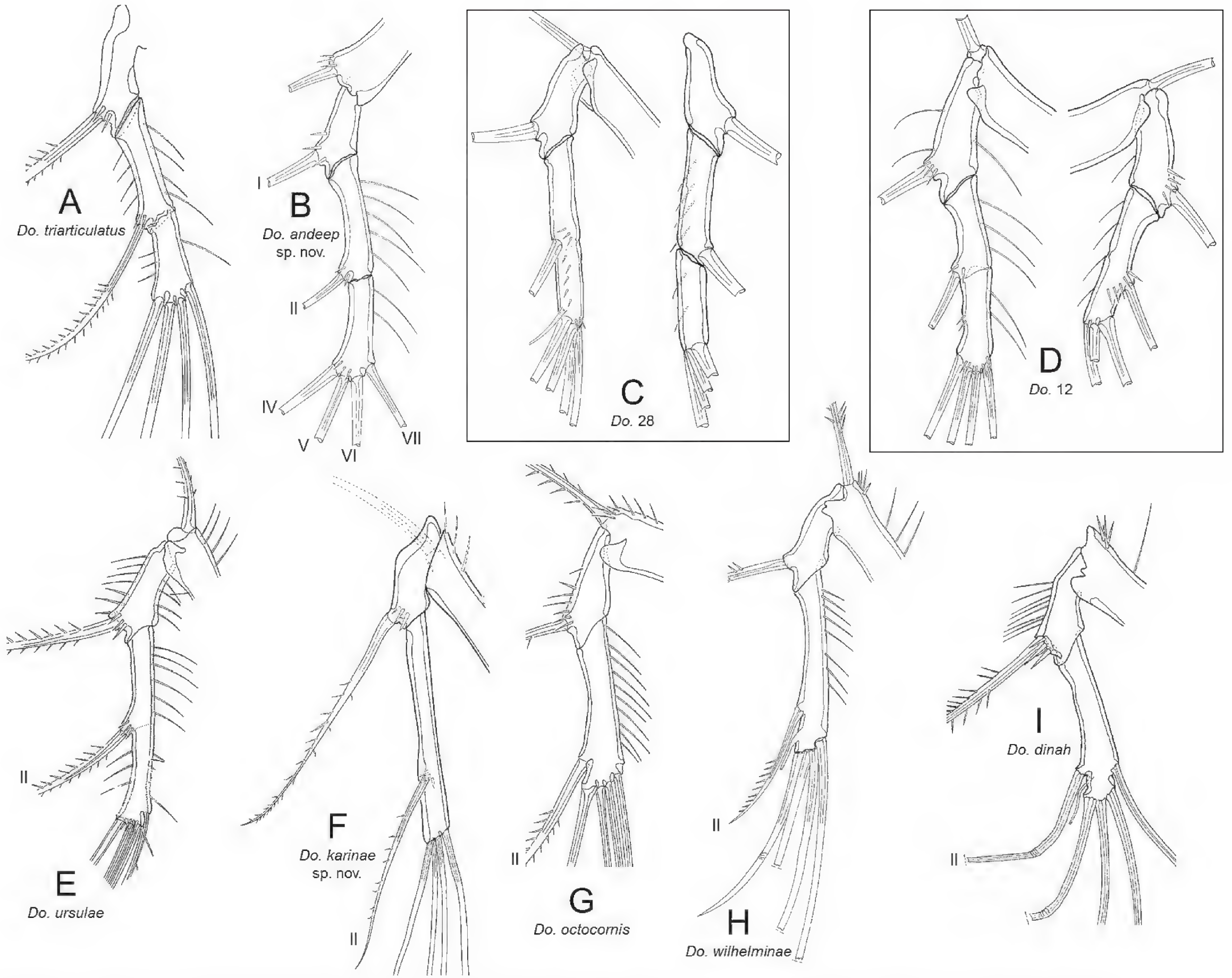

Figure 26. P1 exopods of different *Dorsiceratus* species/specimens, indicating their segmentation. Framed exopods belong to the same specimen.

Dorsiceratus triarticulatus Coull, 1973

In addition to character 7 (see above), recognised by George and Plum (2009) and confirmed here, our study also revealed three potential characters:

28. Md palp: loss of seta 3 or 5 [both setae present];
29. Male P3 exp3 with 2 tube pores [at most with 1 tube pore];
30. Female P5-basoendopod without setae and tube pores [with at least 1 seta and/or 1 tube pore].

Coull (1973) explicitly describes the armouring of the md palpus (character 28) as having 1 inner (basal), 1 outer (exopodal), and 2 apical (endopodal) setae. In the ground pattern of the *Ceratonotus* group, however, the palpus bears 3 endopodal apical setae (cf. George 2021), and this condition is maintained in all representatives of the group except *Touphapleura* Conroy-Dalton, 2001 (George 1998a, fig. 6E), including *Dorsiceratus*. From Coull's (1973) description and the corresponding figure (Coull 1973, fig. 32), it is not possible to determine which endopodal seta (4 or 5) has been reduced. Nevertheless, the reduction itself can be interpreted as an autapomorphy for *Do. triarticulatus*. However, the poor condition of the type material (cf. George 2006a) makes a detailed re-description impossible.

In his description, Coull (1973) does not provide any information on tube pores, neither on the body somites nor on the extremities. However, the partial redescription of the male by George (2006a) showed that there are 2 tube pores on P3 exp3 (character 29) (George 2006a, fig. 16B). This is an almost unique new formation; only the male of morphotype 8 (see above) also has 2 tube pores on P3 exp3. However, as can be easily recognised from the comparison of its description (see above) with *Do. triarticulatus*, they do not belong to the same species. Thus, character 29 is interpreted as an autapomorphy for *Do. triarticulatus*.

Coull (1973: 616) describes the female basoendopod of P5 as "devoid of setae" (character 30). In his re-description of the male, however, George (2006a, fig. 16D) was able to demonstrate 2 setae and 2 tube pores. If Coull's (1973) observation is correct, then the loss of all setae and tube pores on the female basoendopod of P5 has to be assumed to be an autapomorphy for *Do. triarticulatus*.

Remark: Coull (1973) describes and draws the P1 of a female with only 1 instead of 2 apical setae on enp2 (see character 8 above). His indication that this condition was only observed in one of the three individuals he examined, while the other two specimens had 2 apical setae, was overlooked by George and Plum (2009) in their analysis. They erroneously interpreted the reduction of 1 seta as an autapomorphy of *Do. triarticulatus*. Character 8, however, must be regarded as variability and can therefore not be considered here.

Dorsiceratus ursulae George, 2006

The autapomorphies of *Do. ursulae* recognised by George and Plum (2009) (see above characters 9–13) require critical examination. Character 9 (cphth and thoracic somites with fine hairy setules, cf. Fig. 19B) can no longer be considered as an autapomorphy. Several individuals of the material analysed here (Table 2: *Do.* 12, *Do.* 15, *Do.* 24, *Do.* 34) also show such setules (cf. Fig. 19G–I), but with the presumed exception of specimen *Do.* 34, they cannot be assigned to *Do. ursulae*. Character 10 (length of the FR) is also not tenable, because George and Plum (2009) only compared the furcal rami of *Do. ursulae* with those of *Do. octocornis*; they did not consider the furcal rami of *Do. triarticulatus*, which are considerably longer than those of *Do. ursulae*. This character must therefore be disregarded. Also, character 12 is no longer plausible as autapomorphy, as the occurrence of long spinules on the second segment is also detectable in *Do. dinah* and *Do. wilhelminae* (George and Plum 2009, figs. 3A, B; 12A, B)—a fact that those authors overlooked in their analysis. Thus, of the originally five presumed autapomorphies of *Do. ursulae*, only two remain: Character 11 (female A1: 2nd segment with at most 6 setae), which is shared convergently by *Do. ursulae* and *Do. denizae* sp. nov., and character 13 (female A1: 4th segment with at most 9 setae), which can be considered autapomorphic for *Do. ursulae*.

However, we have to admit that it was not possible for us to check the antennulae of all females of the present material. However, the comparison of other characters that we examined in all individuals (e.g., the 2-segmented P1 exopod of *Do. ursulae*, which at first glance still looks like a 3-segmented exopod) proves that at least no other female representatives of *Do. ursulae* occur in the material examined.

Dorsiceratus wilhelminae George & Plum, 2009

Like George and Plum (2009), we are also unable to identify at least one unambiguous autapomorphy for *Do. wilhelminae*. This is mainly due to the fact that only one specimen of the species is available, which is also severely damaged (cf. George and Plum 2009). Well-recognisable characters, by contrast, correspond to the condition that can also be observed in the other representatives of the genus. The only potential autapomorphy could be the following:

31. Endopod of Mx completely reduced and represented by 2 setae only [endopod present at least as a minute, knob-like segment].

Apart from *Do. wilhelminae*, this character only occurs in *Do. triarticulatus* (cf. Coull 1973). However, both species differ clearly in various respects. Apart from the P1 exopod, which is 2-segmented in *Do. wilhelminae* and 3-segmented in *Do. triarticulatus*, *Do. wilhelminae* shows none of the (female) autapomorphies that characterise *Do. triarticulatus*. We therefore assume that the common absence of the maxillary endopod does not indicate

a closer relationship between *Do. wilhelminae* and *Do. triarticulatus*, i.e., it does not represent a synapomorphy for both species. Instead, it is probably convergently lost in them and thus an autapomorphy for both.

For a better overview, all characters for the phylogenetic justification of the genus and the single species are summarised in Table 8. For the sake of completeness, and in order not to confuse the numbering, the characters that have since been discarded are also listed with a strikethrough.

Remarks on some of the characters used

As already stated, it has been difficult for us to find enough distinct morphological characters to clearly distinguish the *Dorsiceratus* species phylogenetically. And when potential apomorphies were discovered, it was difficult or even impossible to determine the direction of reading. We would like to illustrate this with three characters.

The shape of the P1 exopod

A 2- or 3-segmented exopod on the first pair of swimming legs is usually a reliable morphological character for distinguishing species in Harpacticoida. And as can be seen from Fig. 20, the *Dorsiceratus* species also seem to be quite clearly assigned to two groups on the basis of this character: A 2-segmented P1 exopod occurs almost without exception in species that inhabit seamounts, while the deep-sea species are characterised by a 3-segmented exopod. However, the comparison of the individuals examined here also revealed that this character is not as clear-cut as one would assume. Four of the 57 individuals (= 7%), all originating from the deep sea (Tabs 1, 2: *Do.* 10, *Do.* 12, *Do.* 28, *Do.* 46), exhibit a 2-segmented exopod on one side and a 3-segmented exopod on the other (exemplified in Fig. 26C, D). It is obvious that this constellation is not a species-specific character, but rather a morphological malformation. This shows that the formation of 2- and 3-segmented P1 exopods is by no means as consistent as one would like to assume. Rather, these four individuals show that there might be quite a large intra- and possibly also intra-individual variability, which must always be considered in studies of rare taxa such as *Dorsiceratus*.

The shape of the furcal rami

While *Dorsiceratus* species are generally characterised by a remarkable morphological homogeneity with regard to the structure and the armouring of the body and

Table 8. List of characters discussed in the text for the phylogenetic analysis and their assignment to the individual species of the genus *Dorsiceratus* (light grey boxes). Plesiomorphic states in square brackets; characters marked in light red postulated by George and Plum (2009) were discarded in the course of the analysis. Dark grey boxes: Presumed convergences.

No.	Character/Taxon	*Do. andeep* sp. nov.	*Do. denizae* sp. nov.	*Do. dinah*	*Do. karinae* sp. nov.	*Do. octocornis*	*Do. triarticulatus*	*Do. ursulae*	*Do. wilhelminae*
1	Loss of md seta 1 [seta 1 still present								
2	P2 enp2 with 1 apical seta [with 2 apical setae]								
3	P2 exp3 with tube pore [without tube pore]								
4	P4 endopod sexually dimorphic [no sexual dimorphism]								
5	Third abdominal somite with 2 tube pores [with only 1 tube pore]								
6	P1 exopodal seta II geniculated [not geniculated]								
7	P1 basal inner seta minute [seta long]								
8	P1 enp2 with 1 apical seta [with 2 apical setae]								
9	Cphth and thoracic somites with rows of "hairy" setules [no "hairy" setules developed]								
10	FR at least 5.5x longer than broad [at most 4x longer than broad]								
11	Female A1 2nd segment with at most 6 setae [with at least 7 setae]								
12	Female A1 2nd segment with long spinules [lacking spinules]								
13	Female A1 4th segment with at most 9 setae [with at least 10 setae]								
14	P2 exp3 lacking inner seta [with 1 inner seta]								
15	P3 exp3 lacking inner seta [with 2 inner setae]								
16	P4 exp3 lacking inner seta [with 1 inner seta]								
17	FR seta II displaced ventrally [seta II inserting laterally]								
18	FR seta III displaced ventrally [seta III inserting laterally]								
19	Identical to character 11								
20	Female P5 basoendopod with 1 seta [with 2 setae]								
21	Furcal seta I lost [seta I present]								
22	Proximal section of P1 exp2 strongly elongated [section of moderate length]								
23	P5-bearing somite dorsally equipped with strong spinules [spinules, if present, small and fine]								
24	P6-bearing somite dorsally equipped with strong spinules [spinules, if present, small and fine]								
25	1st abdominal somite dorsally equipped with strong spinules [spinules, if present, small and fine]								
26	2nd abdominal somite dorsally equipped with strong spinules [spinules, if present, small and fine]								
27	3rd abdominal somite dorsally equipped with strong spinules [spinules, if present, small and fine]								
28	Loss of mandibular setae 4 or 5 [both setae present]								
29	Male P3 exp- with 2 tube pores [with at most 1 tube pore]								
30	Female P5 basoendopod without setae and tube pores [with at least 1 seta and/or tube pore]								
31	Maxillar endopod fused with basis [endopod distinct]								

appendages, the exact opposite appears to be the case referring to the furcal rami. In fact, almost all of the individuals examined show furcal rami that differ more or less clearly from one another. If one disregards the length of spines or setae and their armouring, it is above all the length of the furcal rami themselves and the ratio to their width that immediately catch the eye. Although the l/w ratio can be divided relatively roughly into ranges (Table 2), the furcal rami can be characterised individually and comprehensively as exemplified in Fig. 27. The question then arises as to whether observed differences are possibly species-specific (which would result in a significant increase in the number of species) or whether there is a large intraspecific variability. Here again the problem arises that variability cannot be recognised due to the great rarity of the species and the small number of individuals found.

The development of tube pores

Like all crustaceans, Harpacticoida also exhibit an abundance of pores that act as exits of glands for their secretions (Lang 1948). If these pores have a flexible tube-like extension, they are referred to as tube pores (Huys and Boxshall 1991). In the Cletodidae these can arise on the P5 and the furcal rami (e.g., Fiers 1991; Gee 1994; Gómez 2003). Tube pores are particularly common in the *Ceratonotus* group, where they are found dorsally and laterally on the body segments, ventrally on the telson, laterally and apically on the furca, and also on various segments of the swimming legs.

This is also the case with *Dorsiceratus*. The representatives of this genus, for example, all have a tube pore on the third segment of the second swimming leg (see character 4 above). This may be an indication that the development of a tube pore at this position is a new formation in *Dorsiceratus*. As mentioned above, however, there are other single species of the *Ceratonotus* group that exhibit a tube pore there, including *Touphapleura schminkei*, which is currently regarded as the most ancestral representative of the group. This raises the question of whether the development of a tube pore at P2 exp3 was already part of the groundpattern of the *Ceratonotus* group but was secondarily regressed within it. This is supported by the fact that derived taxa such as *Echinopsyllus* and *Tauroceratus* George, 2021 have no tube pores, and *Ceratonotus* and *Dendropsyllus* also contain species without a tube pore at the corresponding position. On the other hand, multiple independent formations of tube pores are also conceivable.

As Por (1986) points out, morphological adaptations are also influenced by the ecological conditions to which the organisms are exposed. The development of tube pores could be related to this. Many species of the *Ceratonotus* group are densely coated in detritus when they are found. Tube pores then also enable the release of glandular secretions. A look at the Ancorabolidae shows that tube pores are formed convergently, as those ancorabolid species that also carry a compact "coat" of detritus are always provided with more or fewer tube pores (cf. George 1998b, 2001; Conroy-Dalton and Huys 2000; Gómez and Conroy-Dalton 2002; Garlizka et al. 2022). It is therefore likely that tube pores also evolved independently several times (= convergent) within the *Ceratonotus* group, depending on the ecological conditions and corresponding adaptations of the species.

The fact that within *Dorsiceratus* some species/individuals also bear one or even two tube pores on the terminal segments of the other swimming legs (Table 2) also speaks in favour of the assumption that the tube pores are new formations. The hypothesis that the possession of one or even two tubular pores was part of the groundpattern of the *Ceratonotus* group, which were gradually regressed secondarily—even in the earliest representatives—seems rather implausible to us. We therefore hypothesise here that tube pores formed several times and unevenly within *Dorsiceratus*. However, we must admit that this hypothesis involves a certain amount of speculation. Further findings and morphological, but above all, molecular comparisons must clarify this.

Conclusions

The taxon *Dorsiceratus*, which so far comprises eight species, is currently difficult to establish as a monophylum, and the differentiation of species on the basis of phylogenetically relevant characters is only possible to a limited extent. By means of a morphological comparison of the known species and the inclusion of 57 additional individuals collected in various marine regions, all of which can be assigned to the genus *Dorsiceratus*, we have tried to justify the monophyletic status of that taxon. In doing so, we had to discard some characters previously assumed to be apomorphic but were able to characterise the genus itself and the known species on the basis of autapomorphies (Table 8): *Dorsiceratus* (characters 1–4), *Do. dinah* (characters 5, 6), *Do. octocornis* (characters 23–27), *Do. triarticulatus* (characters 7, 28–31), *Do. ursulae* (characters 11, 13), *Do. wilhelminae* (character 31).

In addition, we have tried to assign the remaining 57 individuals to the known species or to establish them as independent species. We succeeded in doing so for 12 individuals: They are distributed among the species *Dorsiceratus andeep* sp. nov. (1 specimen; characters 14–16), *Do. denizae* sp. nov. (3 individuals; characters 17–20), and *Do. karinae* sp. nov. (8 specimens; characters 21, 22). For the remaining 45 specimens, an unambiguous classification or characterisation was not possible. This was mainly due to the fact that (a) *Dorsiceratus* is characterised by a pronounced morphological uniformity in most of its characters, and the individuals are therefore very similar, but (b) at the same time they differ so much in individual characters (body size, furca, presence of tube pores) that it was not possible to combine individuals even from the same locality into clearly characterisable groups (species) or to clearly differentiate even those from distant locations, and (c) several of the individuals showed damages that did not allow an exact determination of a character state.

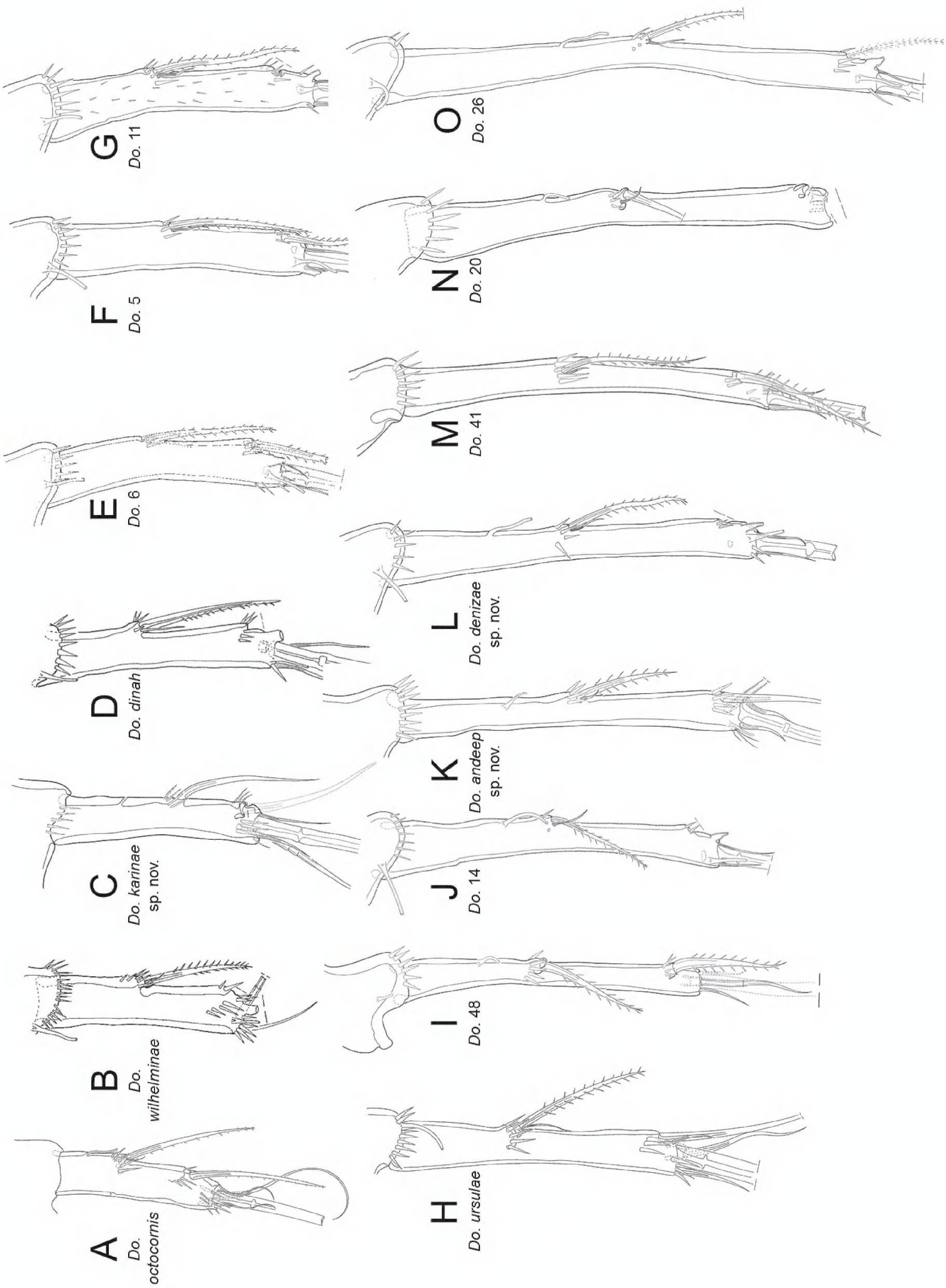

Figure 27. FR of 15 *Dorsiceratus* species/specimens, ordered according to the increasing length of the rami, in order to illustrate the high morphological variability.

For this reason, and in order to provide at least a rough overview, 20 individuals were assigned to eight different morphotypes on the basis of selected (also morphometric) characters and by means of a typologically based similarity analysis. A further male individual shows a proximity to *Do. ursulae*, although this could not be clearly proven. The remaining 24 specimens are summarised in a heterogeneous morpho-group.

Due to the abundance and complexity of their morphological characters, Copepoda Harpacticoida generally provide solid and meaningful data for morphologically based systematic and taxonomic studies, which distinguishes them from other representatives of the meiofauna (e.g., Nematoda). Even closely related harpacticoid species can generally be easily distinguished morphologically, and the vast majority of available features (including the setae on the extremities) can be homologised beyond doubt. This makes the morphological approach a promising tool not only for species description, which is not feasible in any other way, but also for further phylogenetic studies. However, as can be seen from the present case, there are also cases in which morphology can at best provide further clues, but not fundamental elucidation. Our analysis was able to resolve the fundamental phylogenetic ambiguity of and in *Dorsiceratus* only to a limited extent. Rather, it shows that morphological analyses are currently of restricted help in the "darned *Dorsiceratus* case". Instead, integrative taxonomic analyses are necessary, in which morphological and molecular comparisons together will provide clarification.

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